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REFLECTIONS ON BURKE'S *REFLECTIONS ON THE FRENCH REVOLUTION*

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(*Read April 20, 1956*)

THE subject upon which I am about to speak permits me to ride several of my pet hobbies at once. I have at various times risked three generalizations, by no means uniquely my own, yet persuasively confirmed in my own mind by my own study of history. These are: (1) that a revolution is less likely to result from a conspiracy than from the collapse of an old regime; (2) that the American Revolution was a source and an early phase of a revolutionary epidemic that spread to France and then over the world in the century that followed; and (3) that subsequent events may at times shed as much light upon the past as the past upon what follows. These generalizations receive confirmation again, I believe, in an analysis of Burke's views on revolution.

Everyone doubtless has heard of the gentlewoman who, having made her first acquaintance with Shakespeare at a performance of *Hamlet*, was asked how she had liked it and replied: "It was wonderful, it was so full of quotations!" I hope your reaction to my performance today will be the same. I shall quote Burke rather often, and sometimes, I am afraid, the quotations will appear to you unnecessarily lengthy. Their length seems desirable to me in order to make the point I most want to make. That is that this admirable political philosopher and statesman, who has become, above all the things he stood for, a symbol of opposition to the unrealistic and the doctrinaire in politics, became, in his unswerving insistence upon realism, altogether doctrinaire about the importance of being realistic, and hence failed to get a realistic grasp of the early stages of the French Revolution.

Burke's reputation before 1789 had rested principally on his support of four liberal movements. These were the struggle against the abuse of official power by king and ministers inside the United Kingdom; the effort to secure commercial, religious, and parliamentary freedom for Ireland; the plea to effect conciliation with the American rebels; and the long drawn out quest for punishment of those whom he regarded as guilty of injustice in the government of India. His struggle against tyranny in England, Ireland, America, and India might well have led contemporary observers like Charles James Fox and Thomas Paine to expect him to be sympathetic in 1789 with those who, like the Marquis de Lafayette, had fought and bled in freedom's cause in America and now claimed to be fighting in the same cause in France. They were destined to be disappointed. The champion of America in revolt denounced France in revolution.

Burke himself, however, always considered his denunciation of revolution in France consistent with his earlier fights against tyranny. In the closing words of his *Reflections* he said:

> I have little to recommend my opinions but long observation and much impartiality. They come from one who has been no tool of power, no flatterer of greatness. . . . They come from one, almost the whole of whose public exertion has been a struggle for the liberty of others; from one in whose breast no anger durable or vehement has ever been kindled, but by what he considered as tyranny; . . . they come from one who desires honours, distinctions, and emoluments but little; . . . from one who wishes to preserve consistency, but who would preserve consistency by varying his means to secure the unity of his end; and, when the equipoise of the vessel in which he sails may be endangered by overloading it upon one side, is desirous of carrying the small weight of his reasons to that which may preserve its equipoise.[1]

His opposition to the French Revolution, Burke thought, was just such an effort to preserve the

[1] *Reflections on the French Revolution*, 244, London, Dent, 1953 (Everyman's Library). *Cf.* An appeal from the new to the old Whigs, *Works of the Right Honorable Edmund Burke* **4**: 99, Boston, Little, Brown, 1866. The author wishes to express his indebtedness to Hudson, Wilson M., Jr., *An index to the works of Edmund Burke*, typewritten dissertation, University of Chicago, 1947. He wishes also to apologize for the dispersion of his references among several variant editions of Burke's writings; the University of Chicago Library, having been used at various times by Thomas W. Copeland, Robert Maynard Hutchins, Leo Strauss, and other students of Burke, rarely has available a complete set of any one edition.

equipoise of the vessel in which he was sailing and to keep its bearing steady toward the desired goal of just and orderly government. It was consistent with his long and earnest persuasion that the trend in the seventeenth and eighteenth centuries toward geometrical, abstract, and metaphysical solutions of social and political problems could lead only to wrong solutions.

Let us hastily re-examine that trend (since we shall find Burke not altogether unaffected by it). Early in the seventeenth century, René Descartes had taught that the way to find truth was to divest oneself of all one's knowledge, prejudices, and ways of thinking, and to proceed through pure reason to seek one's answers. But if a human being were to divest himself of all his thought, he yet could not deny that he was thinking: "Cogito, ergo sum." And Descartes went on to demonstrate, at least to his own satisfaction, that the thinker, starting from the inescapable fact of thought alone, could arrive at a rational understanding of his problems.

The eighteenth century was the heyday of Cartesians in political thought. Burke, however, felt that positing human awareness of thinking as the prime step toward the solution of human problems was likely to lead to difficulties—to abstractions that had little to do with reality. The thinkers whom he encountered personally in France in 1773 were, he found, proposing exactly the sort of solutions that to his mind had small relation to the ills they were trying to cure.

Burke was, in a sense, an anti-rationalist. As early as his "Speech on American Taxation" in 1774 he had expostulated: "I do not enter into these metaphysical distinctions; I hate the very sound of them." [2] And he asked in his "Speech on moving his Resolutions for Conciliation with America" in 1775: "Alas! alas! when will this speculating against fact and reason end?" [3] In his *Reflections* of 1790, he made still clearer that he had little patience with the handling of social problems in the abstract:

> I cannot . . . give praise or blame to anything which relates to human actions, and human concerns, on a simple view of the object, as it stands stripped of every relation, in all the nakedness and solitude of metaphysical abstraction.[4]

Burke was convinced that, on the contrary, to get the best solutions of the political problems of a people one has to take into account, among other things, the history of that people. He might have been called, had he lived in the nineteenth century, a "historicist"—one of that school which holds that historical experience rather than abstract reasoning provides the correct answers to political questions. As several of his biographers point out, he agreed with the philosophy of Montesquieu, who, you will recall, assigned great weight to history as a factor in the problems and the solution of the problems of mankind. "The spirit of the laws," according to Montesquieu was derived from "the various relations which the laws may bear to different objects." [5] These "objects" were to be found not alone in a people's physical environment but also in their tradition. They determined the institutions, the character, and hence the type of government and customs that a people had and ought to have. This respect for tradition was a far cry from Descartes's indifference to history.

Burke was convinced that tradition, a people's ties with its past, would provide a better answer to its political problems than would abstract reason. Yet his own method resembles somewhat that of Descartes as well as of Montesquieu. In the "Speech on Conciliation with America" he indicated how he set about finding his own answers to political questions:

> In framing a plan for this purpose [how to revive the friendliness of the American colonies] I endeavoured to put myself in that frame of mind which was the most natural and the most reasonable, and which was certainly the most probable means of securing me from all error. I set out with a perfect distrust of my own abilities, a total renunciation of every speculation of my own [so far somewhat like Descartes, but now comes a great difference] and with a profound reverence for the wisdom of our ancestors, who have left us the inheritance of so happy a Constitution and so flourishing an empire, and what is a thousand times more valuable, the treasury of the maxims and principles which formed the one and obtained the other.[6]

In other words, Burke first tried in Cartesian fashion to divest himself of his prejudices, but then he proceeded, not by reason alone from some irreducible premise that remained, but from two historical sources of political truth—the "inheritance" of the British constitution and empire, and "the treasury of maxims and principles" upon which that inheritance was based. The mind once

[2] *Works* **2**: 73, 1889.
[3] *Ibid.*, 45.
[4] *Loc. cit.*, 6.
[5] *The spirit of the laws* **1**: 7, London, Bell, 1914, trans. by Thomas Nugent.
[6] *Works* **2**: 145, 1889.

rationally cleansed of error, he obviously believed, was thereafter guided better by example and precept than by reason.

Burke's concept of an inherited British constitution and empire contained what scholars of a subsequent generation might call the idea of an "organic society." He did not hold with the abstract notion current in the eighteenth century of a social contract rationally derived. Society came rather from divine inspiration:

> He [God] who gave our nature to be perfected by our virtue willed also the necessary means of its perfection—he willed, therefore, the state.[7]

The state was the product of the total experience of a people, the full realization of their destiny:

> Society [i.e. the state] is indeed a contract. . . . It is not a partnership in things subservient only to the gross animal existence of a temporary and perishable nature. It is a partnership in all science; a partnership in all art; a partnership in every virtue, and in all perfection. As the ends of such a partnership cannot be obtained in many generations, it becomes a partnership not only between those who are living, but between those who are living, those who are dead, and those who are to be born. Each contract of each particular state is but a clause in the great primaeval contract of eternal society, linking the lower with the higher natures, connecting the visible and invisible world [i.e. state and church] according to a fixed compact sanctioned by the inviolable oath which holds all physical and all moral natures, each in their appointed place.[8]

If "temporary possessors and life-renters" in a commonwealth should prove "unmindful of what they have received from their ancestors, or of what is due to their posterity," the state would change "as often, and as much and in as many ways, as there are floating fancies or fashions," and "the whole chain and continuity of the commonwealth would be broken." "No one generation could link with the other. Man would become little better than the flies of a summer."[9] It was for that reason that Burke had opposed parliamentary reform in England. Restraint of tyrannical behavior? Yes. Reform of constitutional structure? No.

> Because a nation is not an idea only of local extent and individual momentary aggregation, but it is an idea of continuity which extends in time as well as in numbers and in space. And this is a choice not of one day or one set of people, not a tumultuary and giddy choice; it is a deliberate election of ages and of generations; it is a constitution made by what is ten thousand times better than choice: it is made by the peculiar circumstances, occasions, tempers, dispositions, and moral, civil and social habitudes of the people, which disclose themselves only in a long space of time.[10]

In short, a constitution is the outcome of a people's history, the product of its *Volksgeist,* past and present, and a component of its future.

But the inherited constitution and empire of a nation were not, Burke thought, its only or its best guide for the solution of its problems. The "maxims and principles" on which the political institutions of a people were based were "a thousand times more valuable."[11] They were the essence of its law:

> The science of jurisprudence, [which is] the pride of the human intellect, . . . is the collected reason of ages, combining the principles of original justice with the infinite variety of human concerns.

Without "the collected reason of ages," "no principles could be early worked into habits," and there would be "no certain laws, establishing invariable grounds of hope and fear"; men's actions would lose their course, and their ends would become uncertain.[12]

And still another guide was available to a people seeking wisdom. When Burke in 1775 sought a peaceful solution for the American rebellion, he not only used as arguments telling epigrams and quotations from "the collected reason of ages," from the writings of the great thinkers of the past, but he also tried to draw lessons from the earlier history of England. He described "four capital examples," taken from Britain's experience with Ireland, Wales, Chester, and Durham, that he considered analogous to the American experience. Thus, he employed a third way to use history—examining the successful answers to similar problems in the past in the quest for correct answers to the problems of the present.

So far, then, we have found Burke considering four paths to political wisdom. The first, the rationalistic process, he mostly repudiated. The other three are based upon a philosophy of history.

[7] *Reflections,* 95.
[8] *Ibid.,* 93–94.
[9] *Ibid.,* 91–92.
[10] Speech on a motion made in the House of Commons, May 7, 1782 for a committee to inquire into the state of representation of the Commons in Parliament, *Works* **7**: 95, 1889.
[11] See p. 418 above and n. 6.
[12] *Reflections,* 92.

Of these, he apparently placed (1) the concept of the "organic society" below (2) the science of jurisprudence or "the collected reason of ages," which could be reinforced by (3) parallels in historical experience. But though all three of the good paths had a historical dimension, he had little confidence in the ability of men to profit from their past; it was altogether too easy to choose, from the multitude of the dead, the wrong mentors and to be misled by them. Spanish statesmen, he pointed out, commonly consulted the genius of Philip II, but the issue of their affairs showed that they had not been wisely inspired. A particular affair of state might require for correct resolution something more than the general principles of jurisprudence, the organic order of the society in which it arose, and the lessons derived from comparable affairs in the past. Present realities and the balance of interests in the actual situation also counted heavily with Burke. Hence, in his estimation a studied weighing of immediate and practical advantages ranked high as a source of correct solutions.

To this consideration, which today we call "political realism" or "expedient compromise," Burke gave the name "prudence." "Prudence is not only the first in rank of the virtues political and moral, but she is the director, the regulator, the standard of them all."[13] In his vocabulary the word *prudence* carried none of the derogatory undertone that we might associate with it. All he meant by it was that quality in politics which leads to careful consideration whether a change be worth what it might cost in tangibles and intangibles—to the taking of "a calculated risk," in the language of our day. The true rights of men, in his philosophy, "are their advantages," and, he contended:

> These are often in balances between differences of good; in compromises sometimes between good and evil, and sometimes between evil and evil. Political reason is a computing principle; adding, subtracting, multiplying, and dividing, morally and not metaphysically, or mathematically, true moral denominations.[14]

In his "Speech on Conciliation with the Colonies" (March 22, 1775) he had tried to induce his colleagues in Parliament to apply the principle of prudence:

> It is . . . a very great mistake to imagine that mankind follow up practically any speculative principle, either of government or of freedom, as far as it will go in argument and logical illation. We Englishmen stop very short of the principles upon which we support any given part of our Constitution, or even the whole of it together. . . . All government, indeed every human benefit and enjoyment, every virtue and every prudent act, is founded on compromise and barter. We balance inconveniences; we give and take; we remit some rights, that we may enjoy others. . . . But in all fair dealings, the thing bought must bear some proportion to the purchase paid. . . . Man acts from adequate motives relative to his interest, and not on metaphysical speculations.[15]

When recognition of American independence became opportune, he again urged a prudent calculation of the alternatives:

> A wise man always walks with his scale to measure, and his balances to weigh, in his hand. If he cannot have the best, he asks himself if he cannot have the next best. But if he comes to the point of graduation where all positive good ceases, he asks himself next, what is the least evil; and, on a view of the downward comparison, he considers and embraces that least evil as comparative good. Upon this principle . . . I am not called upon to assert that it [absolute independence] would be good for us. I may admit it as a great evil . . . ; but I have no doubt to assert, that this evil to-day, would be far less than the same evil two years hence.[16]

Prudence thus sometimes dictated a choice among evils.

Even a revolution, Burke believed, might under certain circumstances be justified (though apparently extremely rarely) by "prudence":

> Without attempting . . . to define what never can be defined, the case of a revolution in government, this, I think, may be safely affirmed—that a sore and pressing evil is to be removed, and that a good, great in its amount and unequivocal in its nature, must be probable almost to a certainty, before the inestimable price of our own morals and the well-being of a number of our fellow-citizens is paid for a revolution. If ever we ought to be economists even to parsimony, it is in the voluntary production of evil. Every revolution contains in it something of evil.[17]

[13] An appeal from the new to the old Whigs, *loc. cit.*, 51.

[14] *Reflections*, 59–60.

[15] *Works* **2**: 168–169, 1889.

[16] Lord North and the American war, (n.d.), Fitzwilliams, Charles W., and Richard Bourke (eds.), *Correspondence of the Rt. Hon. Edmund Burke* **4**: 506–507, London, Rivington, 1844. (Mr. Gaetano L. Vincitorio of St. John's University called this passage to my attention.)

[17] An appeal from the old to the new Whigs, *loc. cit.*, 81.

But if revolution is necessary, "it is the first and supreme necessity only, a necessity that is not chosen, but chooses, a necessity paramount to deliberation, that admits no discussion and demands no evidence, which alone can justify a resort to anarchy." [18] Burke thought England's Glorious Revolution of 1688 thoroughly justified because it called for "a small and a temporary deviation" [19] in response to "a grave and overruling necessity." [20] In reflecting on the French Revolution, however, he was afraid that only a small evil would be removed and only at a great cost, and so he doubted that the French Revolution would justify itself.

In 1775, pondering upon the complications arising from revolt in the American colonies, Burke gave an excellent example of his method of political logic. The right answer, he said, was not to be found in "mere general theories of government" or in "abstract ideas of right," but in "the true nature and peculiar circumstances of the object which we have before us." [21] "The collected reason of the ages," he felt, could not provide an adequate understanding of the "peculiar circumstances of the object before us." For one thing, the great minds did not appear to agree on the problem:

> There are deep questions, where great names militate against each other; where reason is perplexed; and an appeal to authorities only thickens the confusion; for high and reverend authorities lift up their heads on both sides; and there is no sure footing in the middle.[22]

For another thing, the law itself may provide only an inexpedient answer:

> The question with me is, not whether you have a right to render your people miserable, but whether it is not your interest to make them happy. It is not what a lawyer tells me I may do, but what humanity, reason, and justice tell me I ought to do. Is a politic act the worse for being a generous one? . . . I am not determining a point of law; I am restoring tranquillity; and the general character and situation of a people must determine what sort of government is fitted for them. That point nothing else can or ought to determine.[23]

He concluded that the problem of America must be decided in the end on the basis of prudence or expediency—upon a calculation whereby the good to be obtained might outweigh the evil that would be eliminated.

To recapitulate, now we have Burke employing five sources of the kind of truth needed for good government: (1) reason, which he either repudiates altogether if it is "metaphysical" or accepts only conditionally if it is coupled with other considerations such as generosity and justice; (2) the organic unity of society, which he appears to accept in the case of the Americans only conditionally ("We Englishmen stop very short of the principles upon which we support . . . our Constitution"); [24] (3) the science of jurisprudence, which may be on both sides and may be interpreted differently by different lawyers; (4) the examples of history, "a fine body of precedents," [25] which require discriminating choice and may sometimes be badly chosen; and (5) the one without which the faultiness of the others might be disastrous, consideration of "the peculiar circumstances," of "the general character and situation of a people." These five paths to political wisdom were all explicitly or, at least clearly implicitly indicated in Burke's writings before 1789.

The outbreak of France's revolution found Burke among the most perturbed. At first he appears to have tried to apply his carefully reasoned method to a dispassionate understanding of the French crisis, but after a few months' suspension of judgment came hysteria. The French, he quickly decided, have rebelled "against a mild and lawful monarch, with more fury, outrage, and insult than ever any people has been known to rise against the most illegal usurper, or the most sanguinary tyrant." [26] This statement, let it be recalled, was written in 1790. The king of France, to be sure, had been placed under constitutional limitations, restricted to a prescribed expense account, and deprived of a great deal of his formerly absolute power and freedom of action. But he had not yet been the victim of outrage upon his person nor was he in any imminent personal danger (although on October 6, 1789, acts of violence had taken place in his presence or close by). As Burke was writing his *Reflections*, the prodigious labors of Lafayette and the loyalty of the National Guard had brought greater order to France than it had enjoyed at any other time since the beginning of the Revolution.

[18] *Ibid.*, 94.
[19] *Reflections*, 15.
[20] *Ibid.*, 25.
[21] *Works* **2**: 109, 1889.
[22] *Ibid.*, 140.
[23] *Ibid.*, 140–141.
[24] See above p. 420 and n. 15.
[25] *Works* **2**: 149, 1889.
[26] *Reflections*, 36.

Therefore, the charge that this was a period of unsurpassed violence is unjust and intemperate. And Burke seems to have altogether forgotten the violence of the English revolutionary experience of the 1640's. The paucity of references in Burke's *Reflections* to the English Civil War is simply amazing. The Glorious Revolution of 1688 is played up again and again, but the Civil War is played down consistently. How could he have forgotten that Charles I had been beheaded while Louis was still safe and still bargaining for a big share of his former power?

Burke's presumption of unparalleled fury in France may perhaps be explained by the inadequacy of his sources. Yet he was by no means uninformed. He had been editor of the *Annual Register* until recently, and the footnotes to his *Reflections* indicate that he still had at his disposal good current literature and other journalistic sources of information. He was in correspondence with several Frenchmen. A recent biographer is under the impression that he perhaps got some of his information from Tom Paine, who perhaps got it from Thomas Jefferson,[27] and both men were in touch with Lafayette, who at this time as commander of the only well-organized military force in France was its most powerful figure. If so, Burke's sources were not all unfriendly to the Revolution, but some were secondhand or thirdhand. I suspect rather that a good deal of his information came from the émigrés who had fled France in the early stages of the Revolution—the ones who were the least likely to see any extenuating circumstances in the events which had compelled them to flee their country. I have no evidence showing what émigrés Burke might have known at the time—the end of 1789—he began to write the *Reflections on the French Revolution*. His persuasion that the revolution was the outcome of an evil conspiracy is reminiscent of the Abbé Barruel's later *Histoire des Jacobins* (1797), and but for the fact that the reproachful cleric did not reach England until after the *Reflections* had been published, one would suspect collaboration. Burke at times was in personal touch with Calonne, who had been one of the more successful ministers of Louis XVI and was now a leading figure and propagandist among the émigrés. Burke cited the works of Calonne several times in the *Reflections;* Calonne came to visit him; and Burke later sent his son to Coblenz to work with Calonne. Some internal evidence also leads to the inference that his reflection on what was going on in France was based upon the reports of émigrés from that country and disgruntled correspondents who remained there. A later American traveler in France was told that Burke's principal informer was an Irish priest named Summers "who wrote him regularly what happened in Paris and colored every event after his prejudices." But the report, if at all credible, seems to have relevance only to Burke's writings after the *Reflections*.[28]

Whatever Burke's sources, his evaluation of them seems to have been determined by a sense of panic. He says himself in his *Thoughts on France*, written some time after the *Reflections:* "Most of the topics I have used are drawn from fear and apprehension."[29] His fears were for England, not for France. You will recall the fuller title of his work—*Reflections on the revolution in France and on the proceedings in certain societies in London relative to that event. . . .* He was concerned with the subversive elements inside England that might derive inspiration from the revolution abroad. In the peroration of the *Reflections*, he pleaded with his fellow-citizens:

> The improvements of the [French] National Assembly are superficial, their errors fundamental. Whatever they are, I wish my countrymen rather to recommend to our neighbors the example of the British constitution, than to take models from them for the improvement of our own. . . . Standing on the firm ground of the British constitution, let us be satisfied to admire, rather than attempt to follow in their desperate flights, the aëronauts of France.[30]

When Burke completed his *Reflections on the French Revolution*, "the aëronauts of France" seemed to him guilty of flighty judgment bound to result in a hard collision with the ground. Earlier he had been less certain of disaster. He had not regarded the fall of the Bastille with the same elation that greeted it generally among Europe's intellectuals, but neither was he at that time fully committed to apprehension of "Parisian ferocity." He was, rather, inclined to suspend judgment. "It is true that this may be no more

[27] Copeland, Thomas W., *Our eminent friend Edmund Burke, six essays,* 147–172 New Haven, Yale Univ. Press, 1949.

[28] Somerville, William C., *Letters from Paris on the causes and consequences of the French Revolution,* 177, Baltimore, Edward J. Coale, 1822.

[29] Thoughts on French affairs, etc., etc., written in December 1791, in *Reflections, op. cit.,* 329.

[30] *Op. cit.,* 243–244.

than a sudden explosion; if so, no indication may be taken from it; but if it should be *character* rather than accident," he reasoned, "then that people is not fit for liberty." [31] Outbreaks of mob violence and civil disorder, however, recurred in France. By November, Burke apparently had decided that anarchy was in the French "character" and not an "accident," and that, therefore, "that people" were not fit for liberty; and so he began the *Reflections*. The first thirty-odd pages are on English affairs and addressed to Englishmen. Only after he has got about one-eighth through his work does he revert to French affairs. By 1790, as the writing of his *Reflections* advanced, he became more and more convinced (although general order was now being re-established in France, and a constitutional solution was being found) that the situation was going from bad to worse.

The first constructive acts of the French Revolution were an announcement of noble intentions to end feudalism and a Declaration of the Rights of Man. For Burke, as for Louis XVI, these were abstractions of the kind for which he had little sympathy. The National Assembly then confiscated the property of the Catholic Church, breaking into the wholeness of the "organic society" for which Burke had such high veneration. So he grew more and more hostile to French "metaphysicians," for whom he had long felt an exasperated contempt anyway. Soon he was thoroughly overwhelmed by the spectacle of these "metaphysicians" trying to establish a Utopian society and instead creating only, as he thought, an inorganic desolation. France's evils, he was fully prepared to believe, came from "one source —that of considering certain general maxims, without attending to circumstances, to times, to places, to conjunctures, and to actors," for "if we do not attend scrupulously to all these, the medicine of to-day becomes the poison of to-morrow." [32]

Outraged by the sight of misguided Utopians helping to produce ghastly ills out of good intentions, Burke apparently forgot some of his own dicta. He apparently forgot that he had declared on one occasion: "In all disputes between them [the people] and their rulers, the presumption is at least upon a par in favor of the people"; [33] and on another: "I do not know the method of drawing up an indictment against a whole people." [34] And yet he did not wholly forget. Burke shared with Rousseau, whom he despised, a certain confidence in the general will. "For," said he, "a man is a most unwise and a most wise being. The individual is foolish; the multitude, for the moment, is foolish, when they act without deliberation, but the species is wise, and when time is given to it, as a species, it almost always acts right." [35] And (in a sentiment strongly reminiscent of Rousseau's often mistranslated pronouncement that the general will, though it may be deceived "is always right-minded" [36]) Burke had once said also: "Wherever the people have a feeling, they commonly are in the right: they sometimes mistake the physician." [37] Burke did not in 1790 indict the whole French people. His opinion was now only that they had chosen the wrong physicians. They had looked for a cure of their ills to theorists, philosophers, "men of letters." "Men of letters" and "literary men" were not complimentary epithets in Burke's language. It was easy for him to think cynically of them. French "men of letters," he believed, were involved in a subversive plot. And they were being assisted by a set of lawyers in the National Assembly who were ambitious for political power, by money-lenders who were trying to take over church property, and by a group of atheists who were seeking to curb the influence of religion upon the French people.

Thus Burke's explanation of the origin of the French Revolution was that it began as a conspiracy of an intellectual and professional elite. Compare this view with his explanation of the American Revolution in his "Speech on Conciliation with America." In the northern colonies of America he had considered widespread religious dissent to be a source of devotion to liberty (and he had found it good); and in the southern colonies the institution of slavery paradoxically played the same role—the freeman upon beholding slavery was strengthened in his desire for freedom. In France, however, religious dissent seemed to him akin to atheism; and serfdom in France did not play the same role as slavery in

[31] Burke to Lord Charlemont, [*ca.* Aug. 6, 1789], quoted in Copeland, 163, and Magnus, Philip, *Edmund Burke, a life*, 185, London, Murray, 1939.

[32] A Letter from Mr. Burke to a member of the National Assembly in answer to some objections to his book on French affairs, 1791, in *Reflections*, 277.

[33] Thoughts on the cause of the present discontents (1770), *Works* 1: 440, 1866.

[34] Speech on conciliation with America, *loc. cit.*, 136.

[35] Speech on representation of the Commons, *loc. cit.*, 95.

[36] *Contrat social*, Book 2, ch. 3. The French is "La volonté générale est toujours droite" (not "la volonté générale a toujours droit").

[37] Quoted in Morley, Viscount John, *Burke*, 64, London, Macmillan, 1923.

America. Another of the main reasons he had discovered in America for the intense quest for liberty was that lawyers were to be found all over the country; but in France, lawyers were undependable, ambitious men who were conspiring to lead the people astray. And the French people had revolted not because they had suffered great provocation, not because the French government had exhibited too late too little of that "magnanimity in politics" which Burke in pleading for conciliation with America had described as "not seldom the truest wisdom." [38] No, he declared, revolution had come to France because the ferocious character of "a swinish multitude" [39] had prepared them to be misled by "the literary cabal" [40] and to take unprecedented action against a truly commendable government. Shortly after publishing the *Reflections*, he classed together as "chiefs of the regicide faction" "the Barnaves, Lameths, Fayettes, Perigords, Duports, Robespierres, Camus's, &c. &c. &c." [41] Mind you, this was in 1791. So far no king has been tried and executed (except Charles I of England). Nevertheless, Burke gives the name of "regicide" indiscriminately to people who have, to be sure, varying and sometimes startling views of the degree of constitutional power to be left to the king but none of whom is as yet wholly anti-monarchical; and, for good measure, he throws in three *et ceteras*.

This is perhaps not the place to re-engage in the classic debate whether the French Revolution was the result of conspiracy or of circumstances. In that debate some respectable scholars have come to a decision that does not satisfy others. My own conclusion on this controversy, presented in more than one place, is that the conspiracy theory does not satisfactorily explain why the Revolution developed as it did. First, the available evidence does not convince me that the several stages of the Revolution were plotted step by step. But even if conspiracy were continuous, it must have been disorganized, feeble, and incoherent, since it was painfully characteristic of the Revolution that its principal leaders should continually disagree and split to form new factions. Even the Jacobins, who were the most abiding followers of "the literary cabal," were constantly changing their membership. If enough evidence could be gathered to reveal a continuous conspiracy, it would still be hard to prove that the conspirators had sufficient coherence and a strong enough following for success by virtue of their effectiveness as conspirators alone. And even if the evidence were to show that a particular group of conspirators had continuity as well as coherence and strength—under a man like Robespierre, for instance (or in a later revolution, Lenin)—it would still probably be inadequate to explain why that group rather than some rival group like the court, the clergy, the dominant social class or the incumbent political faction (any one of which might easily be more coherent and more practiced in collusion than an aspirant intelligentsia) failed where a doctrinaire cabal succeeded. The origin and the course of a profound revolution, I am satisfied, must be sought in "the general character and situation of a people" and "the true nature and the peculiar circumstances of the object which we have before us" (to quote considerations that Burke underlined in his analysis of the American Revolution [42] but in his examination of the French Revolution chose to minimize).

Revolutions, in short, come only partly because revolutionary forces are strong; they come also because conservative forces are either too short-sighted to make timely concessions or too weak to prevent their own collapse. In France in 1789 both short-sightedness and weakness were obvious. Louis XVI made concessions but never in time, and the court, clergy, aristocracy, and army were divided. These groups, which should have supported Louis, disagreed among themselves and with each other, and so other groups, classes, or forces succeeded in displacing them. The initial stages of the French Revolution (and I think that this is true of later stages and of other revolutions as well) are not to be explained so much by the fact (if it was a fact) that revolutionaries were conspiring as by the fact (and it certainly was a fact) that the established order was not strong enough to keep them from putting their program over. The conspiracy or, more probably, the several competing conspiracies on one side in the potentially revolutionary situation were less significant than feebleness on the other in the ultimate collapse of the old regime.

Burke, who had attributed the American Revolution to "circumstances," attributed the French Revolution to "cabal." The inconsistency is all the more glaring in contrast with Burke's apology

[38] *Op. cit.*, 181.

[39] *Reflections*, 76.

[40] *Ibid.*, 107.

[41] Thoughts on French affairs, *loc. cit.*, 323.

[42] See above, p. 421 and nn. 21 and 23.

for the behavior of the English people at the time of the disorders centering around the stormy career of John Wilkes. In his "Thoughts on the Cause of the Present Discontents" (1770), he quoted approvingly a passage from the *Mémoires* of the famous minister of King Henry IV of France, the Duc de Sully: "Revolutions that arise in great states are not a result of chance or of people's caprice. Nothing alienates *the powerful* in a realm so much as *feeble and unstable government*. As for the *populace*, it is never out of a desire to attack that it rises up but out of unwillingness to continue to suffer." [43] Burke then went on to state that what Sully had said of revolutions "is equally true of all great disturbances." [44] Burke found it hard to believe that "this unnatural ferment" of England in 1770 could have been "the wicked industry of some libellers, joined to the intrigues of a few disappointed politicians." [45] That, however, was pretty nearly exactly what he thought in 1789–1790 had happened in France.

Only a few of Burke's biographers, who have argued his consistency pro and con, have grasped this point at all, and none, so far as I know, has assigned to it the significance that I think it has. The difference in his attitude toward the American Revolution and his attitude toward the French Revolution is not to be explained away altogether by the argument that Burke himself advanced in his *Appeal . . . to the Old Whigs*. Burke claimed to have been consistent because he had "always firmly believed that they [the Americans] were purely on the defensive . . . standing . . . in the same relation to England as England did to King James the Second in 1688" against encroachments upon their established rights, while in France "not the people, but the monarch was wholly on the defensive . . . to preserve *some fragments* of the royal authority against a determined and desperate body of conspirators, whose object it was . . . to annihilate the *whole* of that authority [among other things]." [46] Burke, in other words, consistently meant to support the constitutional status quo in both revolutions—in the first instance from violation by crown and Parliament, in the second from violation by the National Assembly. His behavior would perhaps have been still more consistent if he had in fact rebuked the Americans when they did upset the constitutional status quo by declaring their independence. But, although he hoped that independence could be averted and was disappointed when it proved irreparable, the evidence that Burke ever changed his friendly and sympathetic attitude toward the Americans before the French Revolution is very small,[47] while the evidence to the contrary is abundant. In 1777, though by that time he must have known of the Declaration of Independence, he thought Franklin, then in Paris, might yet be induced to negotiate a reconciliation of the colonies, and that the crown might make the necessary concessions to that end.[48] In 1778 he speculated still on a pacification whereby the Americans would recognize the sovereignty of the British crown in return for certain concessions.[49] When the United States instead made an alliance with France, and Spain joined France, he persisted in believing that, in return for a recall of the British troops from America, the Americans would withdraw from the war.[50] When peace was at length contemplated and signed on the basis of independence, he congratulated Franklin on the outcome.[51] Invited to "eat venison in honor of Old England" with John Wilkes in 1788, he promised to attend in his "Blue and Buff" (the colors of the American Continental Army); and to a dinner with the Duke of Portland he proposed to take "the great American Paine." [52] In short, up to the very eve of the French Revolution, Burke may have regretted the loss of the old colonies but he had not yet begun to think of the American Revolution as something in need of apology.

[43] *Works* **1**: 441, 1866. Burke quotes the French words; the translation is mine; the italics are his.

[44] *Ibid.*

[45] *Ibid.*, 438–439.

[46] *Works* **4**: 101–104, 1866. The italics are Burke's.

[47] Somerville, Thomas, *My own life and times, 1741–1814*, 222–223, Edinburgh, Edmonston and Douglas [1861].

[48] A letter to the Marquis of Rockingham, with the addresses to the king, and the British colonists in North America, in relation to the measures of government in the American contest . . . , January 1777, *Works* **6**, 1867; see especially pp. 151–154, 160, and 176–177. *Cf.* his speech in the House of Commons, December 14, 1778, in the *Parliamentary history of England* **20**: 82, London, Hansard, 1814.

[49] Hints for a treaty with America (probably 1778), *Correspondence* **4**: 512–513; Wecter, Dixon, Burke, Franklin, and Samuel Petrie, *Huntington Lib. Quart.* **3**: 319 and 326–328.

[50] Speech of May 31, 1779, *Parliamentary history* **20**: 826–827; speech of Dec. 12, 1781, *ibid.* **22**: 803.

[51] Letter of Feb. 28, 1782, Prior, James, *Memoir of the life and character of the Rt. Hon. Edmund Burke* **1**: 398, London, Baldwin Cradock and Joy, 1826; letter of Aug. 10, 1782, Wecter, 337–338.

[52] Burke to Wilkes, Aug. 18, 1788, in Anon., The great conservative, *Univ. of Chicago Mag.* **46**: 4 and 6, 1953; Copeland, 156.

The conclusion seems inescapable that in 1790 Burke liked the French Revolution less than he had liked the American Revolution in its time because in the interval he had come to be fearful of the current theory of revolution. The French Revolution was in his eyes not merely an unwarranted violation of the French monarchical constitution by literary men, lawyers, and money-lenders. If that had been all, he would doubtless not have liked it but he probably would have considered it little of his business. The trouble was that the French Revolution would not stay at home, that its missionary creed of the Rights of Man was for export. It had already infected "certain societies in London" whose "proceedings" were part of the subject of Burke's *Reflections*. Still, if the danger of infection was the point of departure and the focus of the *Reflections*, it received little space among the two hundred and more pages that were devoted to berating the alleged reforms of France's institutions by the National Assembly.

After the publication of the *Reflections*, Burke became more alarmed regarding the dangers of international contagion. In a letter to the Tsarina Catherine of Russia in 1791 he congratulated her because her sagacity had made her perceive "that in the case of the sovereign of France the cause of all sovereigns is tried,—that in the case of its church, the cause of all churches,—and that in the case of its nobility is tried the cause of all the respectable orders of all society, and even of society itself." [53] After the Revolution gave birth to wars against the "tyrants" and to counterrevolutionary wars, Jacobinism became for Burke "this epidemical distemper" [54] and "the dreadful pestilence which, beginning in France, threatens to lay waste the whole moral and in a degree the whole physical world." [55] By 1796 he labeled the French Revolution the first total revolution: "Before this of France, the annals of all time have not furnished an instance of a *complete* revolution." [56] "Never before this time was a set of literary men converted into a gang of robbers and assassins; never before did a den of bravoes and banditti assume the garb and tone of an academy of philosophers." [57] In one of his last diatribes he called the Jacobins "a sect of fanatical and ambitious atheists . . . aiming at universal empire" by means of a *"civil war"* against "the partisans of the ancient civil, moral, and political order of Europe." Not since the Reformation had a similar ideological conflict threatened to split Christendom so cruelly.[58]

Now at last Burke began to regret the American Revolution. He had come to realize that it had not been a mere domestic dispute between Britons but had been the first wave of a revolutionary surge that would eventually inundate all of the nations of European culture. He first publicly admitted that he had misunderstood the import of the revolt in America when he undertook to reply to the charges of inconsistency in attacking the French Revolution after he had supported the American Revolution. He had never believed, he said, that from the beginning the Americans had "meant wholly to throw off the authority of the crown, and to break their connexion with the parent country." If he had felt that the Americans had rebelled "merely in order to enlarge [rather than to preserve] their liberty," he "would have thought very differently of the American cause." But he had been led by Dr. Franklin to believe that the Americans also wished reconciliation:

> It was, I think, the very day before he set out for America, that a very long conversation passed between them [i.e., Franklin and Burke], and with a greater air of openness on the Doctor's side than Mr. Burke had observed in him before. In this discourse Dr. Franklin lamented, and with apparent sincerity, the separation which he feared was inevitable between Great Britain and her colonies. . . . America, he said, would never again see such happy days as she had passed under the protection of England. . . . Mr. Burke had several other conversations with him about that time, in none of which, soured and exasperated as his mind certainly was, did he discover any other wish in favor of America than for a security of its *ancient* condition.[59]

The impressions Franklin gave Burke were corroborated by conversations with other Americans and by "the reiterated, solemn declarations of their assemblies." So Burke "always firmly believed that they were purely on the defensive in that rebellion." Hence he had advocated appeasement at every step. But others who had favored force

[53] Nov. 1, 1791, *Works* **6**: 116, 1867.

[54] Letter to Sir Hercules Langrishe, May 26, 1795, *ibid.*, 379–380.

[55] A letter to a noble lord on the attacks made upon Mr. Burke and his pension . . . , 1796, *ibid.* **5**: 205.

[56] *Ibid.*, 175.

[57] *Ibid.*, 213.

[58] Three letters . . . on the proposals for peace with the regicide Directory of France, 1796–7, Letter II, *ibid.*, 345–346. The italics are Burke's. On the Reformation see Thoughts on French affairs, *loc. cit.*, 318–322.

[59] Appeal from the new to the old Whigs, *loc. cit.*, 100–101. The italics are Burke's.

and repression had prevailed—with the results that Burke had warned against: loss of the colonies and foreign war.[60]

So far Burke has made a good case for his consistency. He has said that he was in favor of appeasement of revolution in America and against appeasement of revolution in France because they were different kinds of revolution. But in so doing he has begun to admit that he had not fully evaluated the ultimate international significance of the American Revolution. Further recognition of his error came when England, having in 1793 gone to war against regicide France, was being urged in 1796 to make peace. In his flaming tirades against the contemplated "regicide peace," Burke spoke of the French Revolution as having derived, at least in part, from the American Revolution:

> When Louis the Sixteenth, under the influence of the enemies to monarchy, meant to found but one republic, he set up two; when he meant to take away half the crown of his neighbor, he lost the whole of his own. Louis the Sixteenth could not with impunity countenance a new republic. Yet between his throne and that dangerous lodgment for an enemy, which he had created, he had the whole Atlantic for a ditch. He had for an outwork the English nation itself, friendly to liberty, adverse to that mode of it. He was surrounded by a rampart of monarchies, most of them allied to him, and generally under his influence. Yet even thus secured, a republic erected under his auspices, and dependent on his power, became fatal to his throne.[61]

In short, before he died, Burke had formulated a very different view of the American Revolution from that which he had held before 1789. To be sure, that revolution had begun, he still thought, as an attempt to defend the hereditary rights of Americans as subjects of the British crown, but he now complained that he had been misled by Franklin and others, perhaps themselves laboring under a delusion, into thinking it would not become aggressive. Because of the errors of the repression party, it had developed into an international war for the creation of an independent republic, and had provided an example that eventually helped to undermine the French monarchy and threatened the whole Christian order. In fact, at the time of the American Revolution, he now maintained, England was so ripe for revolution that "had the portentous comet of the Rights of Man . . . crossed upon us . . . , nothing human could have prevented our being irresistibly hurried out of the highway of heaven into all the vices, crimes, horrors, and miseries of the French Revolution." But "happily France was not then Jacobinized" and "her hostility was at a good distance," and so "we had a limb cut off, but we kept our Constitution." Nevertheless, had certain so-called parliamentary reforms taken place at that juncture, "not France, but England, would have had the honor of leading up the death-dance of democratic revolution." [62]

In a collapsing Europe, Burke grew more and more disillusioned; even for one so gifted, hindsight was superior to foresight—and in his case more distasteful. His disillusionment is not unlike that which many intellectuals in our own day underwent between 1917 and 1947. He easily blamed ruthless conspirators for the frustration of his earlier hopes. He was entrapped in a perfect syllogism of his own devising, though he himself was probably unaware of either the trap or the syllogism. The major premise of his syllogism was his long-standing conviction that doctrinaires are abominable and that their works are an abomination. The minor premise: The French Revolution is the work of doctrinaires. Hence his conclusion: the French Revolution is an abomination. This reasoning obliged him to hope for the ultimate failure of the French Revolution even before it became clear either that it was a violent departure from the French constitution or that it would fail. The months in which he wrote his *Reflections* were in some ways the most successful of the Revolution. They witnessed the establishment of a constitutional monarchy, of a restricted electorate, of a centralized, departmental regime, and of the *fédérations* of a fairly united and hopeful people—all developments that Burke might well have welcomed under other circumstances. Instead, he saw a dishonored king and queen; a clergy victimized by atheists, moneylenders, and Jews; "a swinish multitude" led by a selfish and ambitious oligarchy of lawyers and men of letters; a "kingdom being hackled and torn to pieces," and held from falling asunder only by financial speculation and "the power of Paris, now become the center and focus of jobbing." [63] He saw a people who had no good reason to overthrow their

[60] *Ibid.*, 101–102; speech of Nov. 16, 1775, *Parliamentary history* **18**: 966.

[61] Letter II, *loc. cit.*, 380–381. *Cf. ibid.*, 372.

[62] A letter to a noble lord on . . . his pension, *loc. cit.*, 180–181. Burke here still ignores the Declaration of Independence, which others would have considered a "portentous comet of the Rights of Man."

[63] *Reflections*, 192–193.

old constitution delivered over to anarchy and the tyranny of the multitude, which must eventually end in a ruthless dictatorship.

Certainly the outcome of the French Revolution justified much of Burke's fear and forecast, and he is therefore entitled to most of the credit for profound prophecy and understanding that he is generally given. Nevertheless, his correct guesses would appear due perhaps as much to panic, bias, and cynicism as to foresight. I doubt whether the French Constitution of 1791, which was being drawn up while he was writing, can be shown to have been intrinsically weak and bound to fail. Who can say whether a better constitution could have been found for France in the circumstances in which she then stood? If, however, Burke had not been stopped by his syllogistic block from considering "the true nature and peculiar circumstances" of the French social structure and "the general character and situation" of the French people, he would, at the time he wrote his *Reflections*, have had to measure and balance several calculations: whether the French legislators could possibly retain undiminished a monarchical power that could be expected in advance to be directed against the very constitution the king was sworn to uphold; whether they could possibly avoid abolishing the privileges of influential nobles who could be expected to use whatever influence was left to them to win back their privileges; and whether they could possibly create a Gallican church without alienating that part of the clergy that would resist church reform to the point of counterrevolutionary activity. If he had striven without passion to understand the circumstances France faced as he had striven to understand the circumstances America faced, if he had applied his own principles and methods of weighing good against evil and bad against worse, he would have said something like this perhaps:

> France is a country that, no matter how unjustifiably, is already undergoing a profound revolution that it may someday regret. We do not wish to interfere in the internal affairs of France. But unfortunately revolutions do not always stay at home. Émigrés and refugees flock into neighboring countries. Sympathy grows for the victims of revolution, and fear that revolution may spread arises among the people who give the refugees asylum. Soon the revolutionary leaders, becoming fearful, in their turn, of their neighbors' sympathy for émigrés and fear of revolution, begin to think of ensuring their own safety. They try to build satellite states and to spread abroad what they call "the blessings of the revolution." Let us, then, beware of getting mixed up in these self-feeding waves of revolution and counterrevolution. Let us so conduct ourselves that, no matter how much we share the émigrés' dislike of their revolutionary regime, we give no reason to that regime to fear harm by our intervention in their domestic affairs.

Burke, unfortunately, did not take a detached tone of this nature. Instead, he preached a personal crusade against what he considered ugly. A year after the *Reflections* he reluctantly admitted that the leaders of the French Revolution had destroyed some evils which cried for destruction, but to his mind they were still in 1791 "cruel and inexorable masters . . . of a description hitherto not known in the world," who had succeeded only "by the practices of incendiaries, assassins, housebreakers, robbers, spreaders of false news, forgers of false orders from authority, and other delinquencies, of which ordinary justice takes cognizance."[64] He became the intellectual anchor of the émigrés' hopes. He gave an eloquent though extravagant literary articulation to the fears and the arguments of the counterrevolutionaries, who until his *Reflections* had had no outstanding philosophical champion abroad. The success of the *Reflections* was both a result and a cause of counterrevolutionary shock. It had one edition a month in England the first twelve months; 30,000 copies are estimated to have been sold before the author's death in 1797;[65] more than 16,000 copies of a "bad [French] translation" were sold within less than a year;[66] and numerous translations and replies (including Paine's *Rights of Man*) and Burke's counterreplies spread its fame. The *Reflections* became the Bible of the counterrevolutionaries of its day, and Paine's *Rights of Man* perhaps crystallized English conservative apprehension still more by its outspoken radicalism.[67]

By December, 1791, Burke for a moment was ready to concede that he was probably trying to stem an irresistible tide. In his *Thoughts on French Affairs* he indicated that the Revolution seemed to him to be over, and he was ready, though reluctantly, to adjust to it:

[64] Letter to a member of the National Assembly, *loc. cit.*, 282.

[65] Morley, John, Burke, Edmund, *Enc. Brit.* **4**: 418c, 1948.

[66] Schmitt, Hans A., and John C. Weston, Jr. (eds.), Ten letters to Edmund Burke, *Jour. Modern History* **25**: 56, 1953.

[67] Winkler, Henry R., The pamphlet campaign against political reform in Great Britain, 1790–1795, *Historian* **15**: 24–25, 1952.

I have done with this subject, I believe, for ever. It has given me many anxious moments for the last two years. If a great change is to be made in human affairs, the minds of man will be fitted for it; the general opinions and feelings will draw that way. Every fear, every hope will forward it; and then they, who persist in opposing this mighty current in human affairs, will appear rather to resist the decrees of Providence itself, than the mere designs of men. They will not be resolute and firm, but perverse and obstinate.[68]

Then the French Revolutionary leaders made not their only mistake but perhaps their gravest one. Largely out of a fear of émigrés and a desire to spread (and in spreading to protect) their revolutionary creed, they engaged in a war with Austria and Prussia that they might perhaps have avoided. The war made impossible a preservation of the new status quo in France to which Burke had momentarily seemed willing to resign himself. Soon came the execution of Louis XVI and England's entry into a coalition against France; and Burke became again indignant and remained to his death bitterly opposed to a "regicide peace."

Burke is not without responsibility for the misfortune he had foreseen—to an extent that no one can estimate accurately but that must have been considerable. He had become a metaphysical doctrinaire in his persuasion that only evil could come from doctrinaire principles and, in so doing, he had helped to create the very evil against which he lifted up his voice. In his unrelenting insistence that the ideal was probably the enemy of the feasible, he had given a philosopher's endorsement to an atmosphere in which neither the ideal nor the feasible could easily prevail. He thus contributed to bringing about the disaster he had predicted. He would have deserved still greater credit for foresight if disaster had come despite his efforts to forestall it, as in the American war, or at least without his having contributed to the passions that made it inevitable. If he was "a great and good man, led into extravagance by a tempestuous sensibility which dominated over all his faculties," [69] if he ended his days trying to sweep back the great revolutionary wave of his day, which he had at first, mistaking its direction and potential, abetted, the reason was a genuine change of heart regarding it. He had persuaded himself that the revolutions of his day were not a historical sequel to the Glorious Revolution of 1688 but a monstrous conspiracy heading toward a new form of tyranny.

[68] Thoughts on French affairs, *loc. cit.*, 330.

[69] Macaulay, Lord, *Historical essays*, 354. New York, Scribner's, 1921.

THE UNDER-DEVELOPED COUNTRIES AND THE STRUCTURE OF THE WESTERN ECONOMY

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(*Read April 20, 1956*)

IN THE midst of a world of rapid change it is not easy to maintain a sense of perspective. Yet it was never more important for the world for which Benjamin Franklin did so much to see itself as others see it, and to realise that the forces of economic and social change have been gathering at a pace unexcelled in human history. The British historian, Arnold Toynbee, declared not long ago that future generations will regard the age in which we live, not so much as a period of great conflicts and technological advances, than as the generation in which society began to accept the welfare of the whole human race as a practical objective. This is a startling pronouncement, but it may well be true. I have had the good fortune to participate recently in discussions in the United Nations and elsewhere on the plans and aspirations of the representatives of countries that have recently assumed independent status, and are anxious to promote the welfare of their peoples. These discussions have underlined the basic difference in approach to this new phenomenon between the western economy and the recently developed and expanding communist economy. It is the purpose of this paper to make some observations on the impact of this fundamental change in the world economy upon the structure of the western economy, and its responsibilities to the new world that is developing around it. I have no doubt that this would have been a topic dear to the heart of our founder and to his contemporary in the United Kingdom, Adam Smith, both of them highly sensitive to the changing world in which they lived. *Felix qui potuit rerum cognoscere causas.* I do not claim to rise to such heights, but I hope that what I am attempting to expound in this brief paper may stimulate others to dwell upon the theme with the attention and scholarship it deserves.

Over recent decades the western economy has emerged from two world wars and a severe depression, and much discussion and controversy over its structure, with a settled shape that commands the respect of the free world. Neither the doctrinaire advocate of control nor the die-hard devotee of private enterprise has triumphed. The economy is a blend of public and private enterprise in differing degrees for different countries; certain measures of control, especially of prices of primary products and levels of earnings and working conditions in industry, are a permanent feature of its structure; the proportion of resources devoted to social welfare is a steadily increasing amount; more and more attention is being given to the development of scientific techniques and research from both public and private sources; an increased attention to social welfare and an expanding production of consumer goods has not seriously interferred with the pace of progress; the gospel of autarchy has been submerged in a growing volume of international trade and a sustained level of international investment. There are differences in emphasis on the way these several elements are combined in the economy as a whole, but the main pattern may be regarded as settled. The question to be considered is whether this pattern will endure in the face of changes in the world economy that have occurred since it emerged.

In western Europe and most members of the Commonwealth of Nations, these tendencies have been more marked than in the North American continent, but there has always been a greater element of public investment in the capitalist economy than the extreme advocates of private enterprise have been prepared to concede. Thus, Adlai Stevenson could declare in his recent book, *What I Think,* "Every new frontier in American progress has been, and will always be, opened by the joint enterprise of business and government." On the other hand, the claims for extending the sphere of nationalisation by socialist and left-wing thinkers have been greatly modified in recent years. This came out very clearly in *New Fabian Essays* published in 1952. This is what one of the contributors, R. H. Crossman, had to say on this point:

The planned economy and the centralization of power are no longer Socialist objectives. They are developing all over the world as the result of the Political Revolution, and the process is accelerated by the prevalence of the war economy. The main task of Socialism today is to prevent the concentration of power in the hands of either industrial management or the State bureaucracy—in brief, to distribute responsibility and so to enlarge freedom of choice.

In the Presidential address to the 29th meeting of the Australian and New Zealand Association for the Advancement of Science in 1952, I dealt at some length with this problem and I take the liberty of quoting from my main thesis:

> We live in a totalitarian age when, in a moment of crisis, we are prepared to enlarge and trust authority in order to defeat those who would wish to impose their authoritarian order upon us. We do this because we have sufficient belief in the inherent capacity of a free society to concede control to authority, when all are agreed that the challenge to freedom must be met by a united effort, and yet be able to regain freedom of enterprise, and the adventure of ideas, when the challenge has been successfully met. Total war required that resources should be mobilised for a grand effort, and it is the prerogative of a free society to establish such controls as it thinks fit in the circumstances in which its continuing existence is threatened. But it would be wrong to assume that controls designed to defend a position can be continued indefinitely to the advantage of the community in other circumstances. I participated actively in the instruments designed to meet the challenge of total war by those who believed in totalitarianism as a permanent force in human history, but I respect the judgment of Herodotus: "While the Greeks were despotically governed, they were not superior in war to any of their neighbours, but when they got rid of their despots, they far surpassed them. This shows that in subjection they did not exert themselves, because they were working for a master, but when they became free each individual keenly did his best on his own account." Observe the words "keenly did his best." They connote a social discipline to which few free societies have attained; the individual cannot do his best in a social order that does not recognise the dignity of the human personality, and we know now that the laissez faire capitalism of the mid-nineteenth century denied to many, perhaps to the majority, the opportunity of developing their latent powers and exercising their rights as citizens of a free world. It was to concede this right to all that restrictions had to be imposed on the few, and that authority and control became an essential feature of a free society. That society is permanent which is capable of reconciling the restrictions inherent in social controls with the full and responsible expression of individual enterprise, and its continuing challenge to accepted standards of social conduct and individual responsibility. Those who believe in control and authority may well pause to enquire whether they have the answer to this dilemma. HE THAT ENDURETH TO THE END SHALL BE SAVED.

If this view be correct it may be anticipated that the structure of the western economy will move further along the line of reconciling the long term interests of public and private enterprise, of working out a balanced relationship between social control and individual initiative, and of providing a large measure of security without thwarting the spirit of adventure. There is wide scope for continued experimentation in a social policy that will guarantee further progress along these lines, and ample scope for speculation in the political philosophy that will ensure success to the social policy. Controversy over basic issues is by no means dead, as witness the episode over the Dixon-Yates contract in the United States, the discussions on the proposed Trans-Canada Pipe Line, or the current controversy between the right and left wings of the British Labour Party over extending the policy of nationalisation to other industries. The free world of the western economy is a complex world and we can never expect significant developments to proceed in a straight line.

But the western economy no longer stands alone, with the rest of the world more or less an adjunct of it, as in the halcyon days of commercial expansion and colonial development in the nineteenth century. Like Gaul, the modern economic world is divided broadly into three parts—the western economy, the communist economy, and the economy of the under-developed countries. The last two are relatively new elements of great magnitude and significance in the world economy as a whole. The shape of the communist economy, like that of the western economy, is now fairly clear and settled in Russia. Within a framework of dictatorship and public ownership, it is characterized by incentives and inequality of earnings, a high rate of saving, much of it forced, great emphasis on investment and development of heavy industry, rapidly increasing output, a surprising devotion to technical training and its application to all phases of industry, massive power in defence and rigid discipline, and absolute control over international trade. While it is not certain how far similar conditions will be established in

China, it is clear that the pattern of the Chinese economy is being built on that of Russia. With this communist economy covering so large an area and embracing a third of the world's population, it cannot but have an important impact on the western economy.

Recent developments have tended to emphasise the impact of the communist economy on the western economy. *First,* there are the striking developments in technology in all fields supported by what is, on any previous standards, a massive and successful training of qualified technicians. This was formerly almost a monopoly of the western economy; it is far from being so today. *Secondly,* the change in political strategy since the death of Stalin, and formally expressed in the proceedings of the recent congress of the Soviet-Communist Party in Moscow, is bound to bring the two economic worlds into much closer contact than before. Whatever the effect on the communist economy, the change cannot but affect both thought and action in the western economy. It is much more of a challenge to the basic structure of the western economy than was the obduracy of Stalin, and it comes at a time when the communist economy has greater economic resources than ever before. These resources are far less than the resources of the free world, but they may not remain far less if progress in the communist economy does not continue to be outdistanced by progress in the western economy. Progress in "automation" is not one-way traffic for either worlds, and we have yet to experience the social impact of technological changes that are rapidly developing into the greatest industrial revolution the world has ever known. *Thirdly,* the western economy cannot but be affected by the impact of the communist economy on the economy of the under-developed countries, also known as the uncommitted world. This will be considered later; here it is only necessary to ask ourselves which economy—the western or communist—is the more effectively based structurally to give aid to the under-developed world. The post-war record and the facts of today leave no doubt that in volume of aid the capacity of the western economy is far greater than that of the communist economy. It is likely to continue so, but man does not live by bread alone, and parts of the "uncommitted world" may find some appeal in the communist techniques, while the communist economy may find its own structure competent to provide a limited amount of aid. The western economy cannot afford to ignore this and therefore to consider its own structure in the light of the new situation.

The shape of the economy of the under-developed countries is not as yet clearly defined as a whole, but certain common features are emerging, and the objective has been established for all to see. It is to improve the standards of production and social welfare in the massive peasant sectors of the economy, to provide modern transport, power resources, irrigation, educational and health facilities, and to promote a balanced and rapid industrialization consistent with stability in the social structure. By these means a rise in living standards and the development of social welfare programmes are to be attained. Given the desire to promote political freedom, perhaps the shape of this economy may be sketched. It will have a larger public sector than the western economy and public investment will be the standard bearer of progress. It will need special forms of investment and financial and technical assistance from abroad, now being developed in the Technical Aid Programme of the United Nations, the International Bank, the Colombo Plan, aid given under Point Four and various forms of bilateral assistance. Most of this has been given up to the present by the western economy, which has been working out a new nexus between the western world and the new independent states that make up the so-called under-developed world. The communist economy has now shown signs of entering the field, and aid of one kind and another to the under-developed world, including investment, is likely to be a feature of the world economy for an indefinite period. Mobilisation of resources and economic planning will also be inherent elements of the under-developed economy, as will some measures of control, especially over the prices of basic commodities and international financial reserves. This will be necessary for the financial stability of the under-developed countries. An increasing proportion of resources will be allotted to health and education and social welfare programmes. In all this change, the deficiencies in savings and in technique will necessitate the development of some new form of association between the countries with resources and the under-developed countries. Progress may well be slower than in the communist economy where dictatorship can force the pace, but it may well be faster than was progress in the western economy in the early period of the industrial

revolution, and it will be much more evenly spread with more attention to social justice.

This last point is of great importance. To the western economy the word "planning" often connotes some lack of faith in private enterprise. To the communist world it represents a beacon light that has guided it out of the wilderness. The word has great appeal to the uncommitted world and has even been sanctified by united action in the Colombo Plan. But, in fact, planning, perhaps unconsciously and less coherently, has been a vital feature of the western economy in the sense that increased productivity has followed greater concerted action to apply science to all phases of human activity. This increased productivity has been drawn upon not only to raise living standards, but to promote a higher level of social welfare in the western economy than the world has ever known. This is precisely what the under-developed countries, that have taken stock of their position, seek to emulate. But they have to start with meagre resources, backward techniques, inadequate public capital facilities and a weight of custom and prejudice that might daunt the most courageous and imaginative of leaders. They must have a plan, and planning on a wide and ambitious front must be their guiding star. It is not a question of finding one or more profitable resources that will attract private capital. It is a question of moving the whole economy in accordance with a well-established plan that will bring balanced development. For this reason the public sector will inevitably be in the front line, and will provide the framework in which private enterprise can operate, consistently with the overriding principle that productivity as a whole is to be raised and social welfare broadened. This is a massive enterprise on the part of both the under-developed countries and those with resources, and in the initial stages success will be impossible without a much larger measure of public investment than has marked the development of countries like Australia and New Zealand. Most people with experience of the problem know that, apart from any question of ideology, this is a basic fact. It is a fact that the western economy cannot ignore. In fact, it has not been ignoring it, even in the United States where the amount of public assistance for capital purposes to under-developed countries far exceeds private investments. It is likely to continue to do so, and it will be necessary for the western economy to develop some structural apparatus through which public capital in the requisite amount may be available to the under-developed countries to support their own fiscal and administrative efforts in the great task to which they are committed.

In all countries the new phenomenon of "death control," itself a product of modern research and better administration, will cause a great increase in population. Estimates show that the world population in 1980 may well be not less than 3,600 million, an increase of 50 per cent on the numbers in 1950. This will be by far the greatest increase in numbers the world has ever known, and it will complicate the problem of development in many countries, especially in the under-developed countries. It is a factor that must affect the relations of the economy of the under-developed countries to the western economy, and throw increased responsibilities on both of them; nor will the communist economy escape a similar impact. It was inevitable that this great increase in population should coincide with the efforts of the under-developed countries, and also the communist world, to adopt modern techniques and to raise living standards. The most spectacular effect of a widespread adaptation of scientific knowledge was bound to appear in the control of mortality in the human race. This will at first impede social and economic progress in many under-developed countries and in the new China. Not so in Russia, which for its area and its historical contacts with the great civilisations of the past, is perhaps the least densely populated area in the world. Even so the Soviet cannot escape some of the consequences of the great and pressing increase in numbers. This will be true in Russia itself and still more so in Russia's uneasy partner in expanding the communist economy. But for the western economy the impending increase in numbers in the under-developed countries, especially those in Southeast Asia, presents a challenge that serves only to underline the thesis already presented. The effort to raise living standards and expand the frontiers of social justice will certainly be made the more difficult by the spectacular increase in the average span of human life, that now seems inevitable in the under-developed countries.

What then may be said of the impact of this total situation on the western economy? It would be folly to assume that it can meet so massive a number of problems without some changes, if not in structure, at least in emphasis. The use of the fiscal weapon will be emphasized in supplying

technical and financial assistance; some added facilities for overseas investment for the public sector of the under-developed economy may be necessary; a plan for "buffer stocks" may be required to impart greater stability to the economies of under-developed countries that rely too much on one or two commodities; new techniques in maintaining short and long term liquidity of international reserves may emerge; private enterprise in the under-developed countries will work within a framework of public investment; a great increase in the proportion of resources devoted to research and technical training will be essential. All this implies that the tendencies of recent years in the western economy to increase the proportion of public investment, to emphasize the importance of the fiscal weapon in public policy, to promote control over commodity prices and stocks, to allot increasing resources for research and training and social welfare, are likely to be emphasized in the years immediately ahead. It may well be asked also whether, in the face of the challenge from the communist economy, and the responsibilities imposed by the economy of the under-developed world, the western economy will be able to afford its policy of "calculated obsolescence" in so many of its durable consumer goods. The resources absorbed in meeting the costs of what may also be called "premature obsolescence" would make a signal contribution to the problems of the under-developed economy, without impairing the capacity of the western economy to continue on its own path of social and economic progress, and to contribute to an expanding world economy. From all this it is clear that some basic thinking will be necessary as to the respective parts public and private enterprise should play in the new world of which we are now on the threshold.

These are some of the problems that a survey of economic trends inevitably raises. If we say with Adam Smith that economics is "a branch of the science of a statesman or legislator," the study of economics in the modern world is pregnant with meaning. Nor is there any way of escape and we have to say with Horace:

Nam tua res agitur, paries cum proximus ardet. (It is your own interest that is at stake when your next neighbour's wall is ablaze.)

AMERICAN PRODUCTIVITY: CAUSES AND EFFECTS

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(*Read April 20, 1956*)

NEARLY all Americans, as well as most informed foreigners, agree that the United States is the "richest country in the world," but there is no consensus as to whether this is due to American genius or to American good fortune. Whatever the reasons, it is unquestionably true that the productivity of the American economy, and the standard of living this productivity makes possible, are higher today than ever before, and far above the highest level any other country has ever been able to achieve. With less than seven per cent of the world's land area and little more than six per cent of the world's population and manpower, we produce and consume in the United States more than one-third of the world's entire output of goods and services. In factory goods alone our proportion is much higher—close to one-half of the world total—and measured by national income, the American proportion is not far from forty per cent.[1]

Thus the typical American enjoys a standard of living some six times higher than the average of the two and one-half billion people of the world, and of course many times that of the hundreds of millions who keep the world average as low as it is. The aggregate income of the 167 million Americans today probably exceeds the combined income of the six hundred million people living in Europe and Russia, and far surpasses the total income of the more than one billion inhabitants of Asia.[2]

However, income estimates for the subsistence economies of Asia are notoriously unreliable, and comparing their meager incomes with those of an advanced industrial nation may somewhat overstate real differences in well-being. Comparisons of American standards with other urban-industrial countries are more significant, and, even here, disparities are striking. Only in Canada, Australia, New Zealand, Switzerland, Sweden, Denmark, and the United Kingdom did per capita income a few years after World War II rise to as high as sixty per cent of the American average. Even in relatively advanced European countries, such as France and Italy, and in the most advanced South American countries, average income is considerably less than half what it is in the United States. In the less developed countries of Europe, such as Greece and Spain, the average is, of course, much lower.[3]

International comparisons of national income and of wages and salaries, expressed in monetary units, are never precise measures of real differences in welfare, because of difficulties in translating one currency into another and of differences from one country to another in the way people live and in the taxes they pay. Such difficulties can be partially avoided by comparing the buying power of wages for various commodities and articles of common consumption in all countries. Many such comparisons have been made, but only two can be cited.

In 1950 our Department of Labor made a careful study of the working time required in the United States and in nineteen other countries to earn enough to buy one pound each of eight staple foodstuffs (such as flour, butter, cheese, potatoes, etc.). The results showed American workers not only far ahead of those in other countries, but in a relatively better position than before World War II. The American worker had to put in ninety-eight minutes, or a little more than one hour and a half, to earn enough to buy this eight-pound basket of food. This compared with an average of about six hours for the other nineteen countries, and more than fourteen hours for a worker in the Soviet Union. Even in Australia, which compared most favorably with the United States, more than two hours' work was required.[4]

Another postwar study made by the French economist, Jean Fourastié, shows the purchasing power of the wages paid common labor in the United States far ahead of that in twenty-eight other countries, not only for foods but for a wide

[1] Dewhurst, J. Frederic, and others, *America's needs and resources : a new survey*, 892, New York, Twentieth Century Fund, 1955.

[2] *Ibid.*, 892.

[3] *Ibid.*, 892.

[4] *Ibid.*, 896.

range of other goods and services. About the only exception, significantly enough, was for personal services, such as haircuts and maid service, which are little affected by mechanization and in which presumably labor productivity is much the same all over the world. The cost of a man's haircut, for example, was identical in the United States, Italy, Switzerland, and Uruguay—the equivalent of one hour's earnings for common labor. But the purchase of a pair of shoes, which was more or less typical of other factory-made articles, required four hours' work in the United States, but cost from three to eight times as much in the other three countries.[5] It appears that efficient factory methods, rather than manual skill or "labor efficiency," are the predominant causes of high productivity, low prices, and a high standard of living.

These comparisons of wage-purchasing power are only indirect measures of labor productivity, but what they show is fully confirmed by other studies of output per worker and per man-hour in different industries. All of these studies make it clear that productivity and purchasing power are much higher in the United States than anywhere else in the world. The advantage enjoyed by the average American, both in what he produces and in what he can buy with his earnings, varies from some fifty or sixty per cent in the case of a few advanced countries to several hundred per cent for the relatively underdeveloped countries of Europe, and much more for many other parts of the world, where industrial and agricultural methods are so primitive and living conditions so wretched as to defy comparison with our own. Because he is able to produce so much, the typical American today takes for granted a level of material well-being beyond the comprehension of the vast majority of the world's people. Too often our high standard of living is symbolized in terms of automobiles, electric refrigerators and television sets—which overlooks the fact that such American necessities as window screens, paved streets and pure water and milk are luxuries unknown to most of the rest of the world.

And, of course, the present-day American lives on a much higher material level than his parents did a generation ago, and is vastly better off than his grandparents of the nineteenth century. Average per capita national income last year was over $1,900—which was more than a fourfold increase over 1850, when per capita income in money of today's purchasing power was about $450.

Because this great advance in material welfare accompanied a steady decline in working hours, it reflects even larger gains in hourly productivity. The 1850 worker, working long hours, turned out in each hour of work about thirty-eight cents' worth of goods—in terms of what money will buy today. By 1900 productivity had more than doubled, to eighty-four cents per man-hour, while the period since the turn of the century has brought an even larger increase—to nearly $2.50 per man-hour last year.[6] Today's worker puts in a forty-hour week, and his family enjoys a standard of living beyond the imagination of his grandparents because he can produce as much in ten minutes as his 1850 ancestor could in an hour.

Thus, labor productivity in the United States today is not only about six times the present world average, but approximately six times what it was in our own country a century ago. And there is no reason—barring the devastation of atomic war—to believe that gains in productivity and advances in the standard of living will be any less rapid in the foreseeable future than they have been in the past. There is some evidence, in fact, that technological progress is causing productivity to increase at an accelerating rate. But even the average gain in output per man-hour during the past century would give startling results if long continued. With this rate of gain for another century, we would be able to produce as much in one seven-hour day as we produce today in a forty-hour week. If this should happen, however, it seems reasonable to assume that our descendants will not be satisfied with what they can produce by working one day a week, nor will they have enough time left over to consume all they can produce by working a forty-hour week.

On the contrary, if this upward trend in our ability to produce continues, we shall continue to take part of our potential gain in the form of shorter working hours and more leisure, as we have in the past. A century ago the work-week averaged close to seventy hours and the Sabbath was in fact, as well as name, a day of rest. By 1900 we were still working a ten-hour day and a six-day week. After World War I, the work-week dropped to forty-eight hours, but Saturday was still a work-day for most people. Only after World War II came the five-day, forty-hour work week. These changes, together with the spread of paid

[5] *Ibid.*, 897.

[6] *Ibid.*, 902; calculated for 1955 on same basis.

vacations, have more than doubled the amount of leisure time for the average worker since the turn of the century.

During the past half-century, a little less than two-thirds of the potential increase resulting from advancing productivity has been represented by additional goods actually produced, and a little more than one-third by shorter working time and more leisure. If these proportions prevail in the near future, we can expect by 1975, if not before, not only a much higher per capita income for a larger population than at present, but a four-day work-week and a three-day weekend.

The ultimate reasons for the rapid progress and economic superiority of the United States are many and complex, and there is no complete agreement even on the immediate causes. Many foreign observers unhesitatingly attribute our higher level of productivity and well-being to an abundance of fertile land and natural resources. These are clearly significant, especially in the case of fuel and energy materials, but it is doubtful whether they are of controlling importance. After all, the United States possessed greater resources a century ago, but our productivity is vastly highly today. If natural wealth were the principal source of productivity and prosperity, it would be hard to explain how Switzerland, with meager resources, has been able to achieve a high standard of living; or why Rumania, with large oil reserves, makes little use of automotive power; or why the steam engine is a rarity in China in spite of her extensive coal deposits. On the basis of natural resources alone one would expect Bulgaria to have a higher standard of living than Denmark, Poland to be more prosperous than Holland, and Yugoslavia to be more productive than Sweden, whereas the opposite is true in each case. For that matter, Russia has a land area twice as large as ours and certainly rivals the United States in its reserves of minerals and other resources. Yet Russia until recently failed to exploit her natural wealth, and even after three decades of intensive industrialization remains a country with low productivity and a low standard of living.

The fact that we produce so much of the world's goods with such a small share of the world's manpower finds its immediate cause not so much in abundant land and resources as in the dynamic character of American technology, centering in the application of inanimate energy and mechanical methods in all phases of American industry. It is no accident that American leadership in labor productivity and in per capita income is roughly paralleled by our heavy consumption of coal, oil, and other forms of inanimate energy. Annual consumption of mineral energy in the United States is higher than in any other country—equivalent to about eight tons of coal per capita, compared with about two tons per capita in such countries as France, Netherlands, and Poland, where average income is from one-third to one-half what it is in the United States, and less than one-fifth of a ton in such poverty-stricken countries as Egypt, India, Pakistan, and Burma. Such statistical evidence merely confirms common observation that ours is a "high energy civilization," where the worker has the use of far more numerous and powerful power-driven tools and equipment—not to mention more light and heat—than his colleagues in other parts of the world or than his own predecessors.

For we have not always been a high energy civilization. In 1850 the total rated capacity of all the steam engines and other prime movers used to supplement the work performed by human beings in mining, manufacturing, transportation, and communication in the United States was 2.5 million horsepower—less than half as much as the 6 million muscular horsepower provided by horses, mules, and other work animals. By 1900 the total of mechanical horsepower had increased to 46 million, and by 1952 to 360 million, while nearly all the work animals have long since succumbed to technological unemployment. Mineral, or "mechanical," energy accounted for less than one-third of all the physical work done in the United States a century ago, for more than two-thirds in 1900, and for nearly 99 per cent today. The work done by the muscle power of animals and men dropped from two-thirds of the total in 1850 to little more than one per cent today.[7]

These vast changes help to explain how we have been able in a century to multiply our net output—as well as our consumption—of goods and services about thirty times, with less than a ninefold increase in the labor force and about five times as large an input of human effort, as measured by total man-hours worked. In other words, one man with today's power-driven equipment and other mechanical and chemical aids can produce as much in a forty-hour week as three men working seventy hours a week with the primitive tools of a century ago.

[7] *Ibid.*, 912.

Of course our technology is not limited to the substitution of mechanical power for muscle power. Specialization of tasks and division of labor appear to be carried much further in American industry than in other countries. The efficiencies of mass production would not be possible without a mass market, which in turn is supported by consumer acceptance of standardized products. This simplification and standardization of products designed for a continental market would account for higher productivity in American establishments, against foreign enterprises using identical equipment in supplying their smaller national markets and their much smaller class markets.

It is easy to see how a dynamic technology, lavish capital investment, and the development of mass markets help to account for high and rising productivity. It is more difficult to understand why American progress has been so much more rapid than that of even the largest and most favored industrial nations. In part, this rapid progress is due to geographic and demographic factors—to the fact that most of our history has been characterized by a plenitude of fertile land and a chronic scarcity of labor. Denied an abundance of muscle power, American industry and agriculture have applied labor-saving methods and machinery on a scale never equaled in any other country.

Perhaps more important, however, are the human and institutional influences that help to account for the technological factors. One of these, of which foreign visitors are immediately aware, is the more receptive attitude of American industrial management, shared by American workers and consumers, toward experimentation and change, toward the substitution of new products and methods for old ones, toward progress and expansion, even at the risk of disappointment or loss. European observers—though not always American economists—are quick to attribute American dynamism to what the English economist Graham Hutton describes as "the much greater degree of competitiveness in American business" which, he concludes, "leads to a much higher average of productive efficiency, through a much higher degree of managerial competence." [8] One of the French teams brought to the United States under the ECA program observed that a "truly competitive state of mind" made American businessmen "more ready to seek ways of lowering . . . costs, and less ready to seek ways of restricting competition." [9] One of the most thoughtful English journals, *The Economist,* concludes that "The real secret of American productivity is that American society is imbued through and through with the desirability, the rightness, the morality of production." [10]

If, in truth, capitalism in America is more individualistic, competitive and dynamic than elsewhere, the explanation, as in the case of other human institutions, may be found in the people who created it. America was settled by people of every European strain. No other nation has ever been created in so short a time from the intermingling and fusion of so many racial strains and national cultures. Whether it is true, as one geneticist suggests, that this mixture of stocks is producing the same heterosis or "hybrid vigor" that results from crossing different strains of agricultural plants and animals, the character and diversity of immigration have undoubtedly contributed to American cultural and technological vigor.

Even though the heavy immigration from Europe was free and unrestricted, the immigrants were in fact a highly selected group. Since they came on their own initiative, they were self-selected on a basis that ensured a larger-than-average proportion of risk-takers, of non-conformists and innovators, of those dissatisfied with things as they were and anxious to welcome change if it promised improvement. Coming to the United States, as they did, from varied backgrounds, they brought with them many different occupational skills and a knowledge of various industrial techniques. Interchange of ideas in a highly favorable environment and within a fluid society that had not acquired fixed industrial traditions helped to create an inventive and dynamic technology. Whether the Americans are hybrids or not, Yankee ingenuity is a hybrid product.

[8] Hutton, Graham, *We too can prosper,* 98, London, George Allen & Unwin, Ltd., 1953.

[9] Productivity, source of well-being, 11, The French Association for the Improvement of Productivity, 41 Quai Branly, Paris, France.

[10] The riddle of prosperity, *The Economist,* 80, July 11, 1953.

THE ROYAL MYTH IN ANCIENT EGYPT

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(*Read April 20, 1956*)

In the pyramid temple of the Fifth Dynasty pharaoh named Sahu-Re there is a formal proclamation of victory over the Libyans. A scene showing the pharaoh finishing off the Libyan prince is accompanied by the legend, "Smiting the Ruler of Libya." The scene has further circumstantial detail in a precise listing of the animals captured on the campaign: 123,440 cattle, 223,400 donkeys, 232,413 goats, and 243,688 sheep. As witnesses to the ceremonial sacrifice of the enemy prince stand three captured Libyans, a woman and two small boys. Surely they must be the princess and two princelings of the Libyan ruling family, forced to be present at the celebration of Egypt's triumph. Their carved figures are accompanied by their names: the woman was Khut-iotes, and the boys were Usa and Uni.[1]

Very well. When, some fifty years ago, this proud assertion was discovered and published, we said that we had here a historical record. In the twenty-fifth century B.C. the pharaoh Sahu-Re undertook an expedition against Libya. The booty in domestic animals was very high. The Libyan ruler was captured, together with his family, and he was ceremonially slaughtered in the presence of his family. Here was an established fact of history.

Then about twenty years ago the pyramid temple of Pepi II was excavated. He was a Sixth Dynasty pharaoh, who reigned about two hundred years after Sahu-Re. Here was a depiction of Pepi II bashing a Libyan over the head. Here was animal booty, even though the wall is now too broken to show whether the captured animals were listed in numbers. And here were a Libyan woman and her two small boys watching the sacrifice of the Libyan prince. Over their heads appear their names, the mother Khut-iotes and the boys Usa and (U)ni, just like the names two centuries earlier.[2]

There have recently been published the results of an Oxford expedition to the Sudan, to a place named Kawa, more than a thousand miles south of the monuments I have already mentioned. Here lay a temple of the Ethiopian pharaoh Taharqa (Biblical Tirhakah), who lived in the seventh century B.C., thus eighteen hundred years later than Sahu-Re. There is a scene of the pharaoh trampling upon his Libyan enemies. Captured animals are shown, although again the numbers, if any, are now lost from the wall. And here again a woman and two boys are forced to watch the Egyptian triumph. Again the woman is named Khut-iotes, the boys are named Usa and Uni.[3]

Thus the identical scene appears over a range of eighteen centuries and a thousand miles. In the later two of these three cases we must be dealing with a tradition, rather than a historical record. If that be the case, then it is also possible that the earliest of the three had also been a tradition based on older documents lost to us. This apparently specific record of a conquest over the Libyans may have had a long reiterative history.

What then happens to these documents as historical records? Well, at some unknown time there must have been an original basis of fact, so glorious and so normative that it provided the worthy statement of royal conquest for all succeeding generations. Every pharaoh conquered the Libyans in the same way that the first of this series conquered them—down to the last corroborating detail of the names in the Libyan royal family. It is as if every Roman emperor after Aurelian felt it appropriate to drag a queen Zenobia of Palmyra in triumph through the streets of Rome.

We possess a long and circumstantial account of a military campaign by the pharaoh Thut-mose III about 1475 B.C.[4] We read that this record was

[1] Borchardt, Ludwig, *Das Grabdenkmal des Königs Sahu-re.* Band II. *Die Wandbilder,* Blatt 1, Leipzig, 1913.

[2] Jéquier, Gustave, *Le monument funéraire de Pepi II.* Tome II. *Le Temple,* pls. 8, 9, 11, Le Caire, 1938. The name (U)ni, although written defectively, is obviously the same as Uni.

[3] Macadam, M. F. Laming, *The temples of Kawa. II. History and archaeology of the site. Plates,* pl. XIX, Oxford Univ. Press, 1955.

[4] Most recently studied by R. Faulkner in *Jour. Egyptian Archaeology* **28**: 2–15, 1942. Translated in *Ancient Near Eastern texts relating to the Old Testament,* ed.

extracted from the day-book of the chief clerk of the army. We are given details of the Egyptian army's march from Egypt into Asia, and we are told about a military conference when they were close to the enemy. In that conference the generals gave sound strategic advice about a precarious mountain pass, but Thut-mose III swept aside their advice in favor of his more daring plan. We are told how his plan of advance succeeded. The locations of the two armies before battle are specified. Then suddenly the record as history collapses. The Egyptian king appeared on the battlefield, and the enemy immediately broke and ran. After all, what else could a faithful Egyptian record say about a conflict in which the Egyptian army was led by a god? When he made his epiphany as a warrior, the fight was over.

Let us shift to a different set of documents. The Egyptian campaigns of conquest in Asia in the fifteenth century B.C. required energy, endurance, and courage. They required that the pharaoh set for his subjects the example of vigor and skills in the arts of warfare. Thus for four generations we have records of the king's skill in archery and horsemanship. About 1430 B.C. this culminates in a series of statements about the colossal achievements of the pharaoh Amen-hotep II in those athletic exhibitions which demonstrate strength, endurance and accuracy. There are several documents about his surpassing driving force with the bow and arrow.[5] In the past twenty years two stelae of Amen-hotep II have been discovered, with an extended boast of his athletic prowess. Let me give three samples of his ostentatious demonstrations of skill and power in the presence of witnesses.[6]

Amen-hotep II declares that he once pulled the stroke oar in a boat of two hundred oarsmen. After they had rowed about one kilometer, the two hundred men "were weak, their bodies were limp, they could not draw a breath, whereas his majesty was (still) strong with his ten-meter oar." He continued to row another five kilometers, "without letting down in pulling. Faces were bright at the sight of him when he did this." Deliberately we are given the picture of the entire crew collapsed at their oars, while the king alone took the boat over a long course. Since his pulling from one side would only produce a circular course, we must interpret the text as meaning that others in the boat were encouraged by his example to pull their oars, even though they were weary. When the flattering witnesses remarked that the king was the only real oarsman in the boat, the text enlarged his prowess to a unique feat.

On another occasion Amen-hotep II went to a parade ground, where four copper targets had been set up, each about ten meters distant from its neighbor. He mounted his chariot and drove his horses down the course, shooting at one target after another. He hit each target with his first try, with such force that the arrow went completely through and dropped to the ground at the back—and this despite the fact that each target was of copper nearly three inches thick. The text says solemnly: "It was really a deed which had never been done nor heard of by rumor: shooting at a target of copper an arrow which came out of it and dropped to the ground—except for the king," Amen-hotep II.

And an example of sweeping bravura. On a military campaign in Asia, the Egyptian army took about three hundred captives. Around these prisoners they dug two ditches and filled the ditches with fire. Then all night long, "his majesty kept watch over it until daybreak, with his battle-axe in his right hand, alone, without a single person with him, for the army was far away from him." Even though we discount the word "alone" as we discounted it in the case of his rowing alone, this was a complete expression of the myth of the invincible Egyptian pharaoh, the myth that he could achieve beyond mere mortals, because he was a god.

Although the examples I have given may be the more vivid, they are typical of the assertion of the superhuman power and effectiveness of the pharaoh. It was not the Egyptian army which conquered, it was the god who led that army, because he was divinely more powerful, more skilled and more commanding than mere men.

And yet the texts of Amen-hotep II assert that these extraordinary feats were undertaken in the presence of witnesses. In the case of the Libyan princess and her two sons, we may say that we are dealing with tradition rather than visible fact. In the case of the muscular exhibitionism of Amen-hotep II, it is clear that his contemporaries

by James B. Pritchard, 234–238, 2nd ed., Princeton Univ. Press, 1955.

[5] See, for example, Van de Walle, B., Les rois sportifs de l'ancienne Égypte, in *Chronique d'Égypte*, No. 26: 234–257, 1938.

[6] Hassan, Selim, in *Annales du Service des Antiquités de l'Égypte* **37**: 129–134, pls. I–II, 1937; A. M. Badawi, in *ibid.* **42**: 1–23, pl. I, 1943. Translations in *Ancient Near Eastern texts*, etc., 244–247.

saw some demonstration of skill and power. Should we transfer our modern skepticism back to ancient Egypt and assume that they also had an indulgent element of skepticism? Should we think of modern professional wrestling, with a dramatic contest but a predetermined conclusion, to apply to the ancient scene? I think not.

The modern is forced to speculate on the answers to the problems of actuality and mythology, fact and fiction, skepticism and faith. But there are certain guideposts which may point to an answer.

In the first place, we face a similar problem in studying the depiction of ancient Egyptians in their art. Here a debate has centered upon the word "portraiture." Is it possible to discern a delineation of the individual in statues, reliefs, and paintings, or did art ignore individual characterization in favor of the ideal stereotype, the eternally youthful and tranquil Egyptian, who looked just like every other eternally youthful and tranquil Egyptian?

The truth is not to be found at either extreme. To the casual eye, all Egyptian statues of a certain period may look just about the same. Careful analysis brings out individualism, for example, that all the representations of Hem-Iunu have the same beaked nose and that all the depictions of Montu-em-het show the same slight lifting of the left eyelid.[7] There was a portrait overlaid with idealization. Under the important myth that Hem-Iunu was eternally handsome and strong lay the acknowledged fact that he had a prominent nose. The truth was not mere photographic truth. The truth was a larger and more commanding truth that men do not wither and die, that men live forever in a noble vigor. This truth of faith was more important than a mere truth of the senses.

So also there was probably a basis of fact for the myth of the all-strong and all-successful pharaoh. Under the demands of his day Amen-hotep II had been trained to be strong and skillful, so that he might give public demonstrations of his abilities. We need not accept the narrow truth of his rowing a boat five kilometers by himself or of his driving arrows through three inches of copper. We can accept the larger truth that men who had seen his demonstrations of physical prowess loyally believed that he was superhumanly strong and skillful. They ardently wished to believe.

Similarly, the narrower truth is that Pepi II and Taharqa did not sacrifice the husband of the Libyan princess Khut-iotes, the father of the boys Usa and Uni. The larger truth was that any pharaoh was the same conquering god that he always had been. At some point in his divine career he had conquered that Libyan prince, and so of course he still does so.

In our modern times we have seen frightening examples of the belief in superhuman powers. Amen-hotep II in athletic exhibitionism recalls Mussolini jumping his horse over a flaming hurdle. Thut-mose III brushing aside the counsel of his generals and imposing his own superior wisdom recalls the overbearing strategy of Hitler. Again, patriotic fervor is always fighting the same old battles of Waterloo or Second Manassas or Gettysburg, confident that our power is still the same, just as the pharaoh of Egypt bashed that same Libyan on the head for eighteen centuries.

We also have more benign parallels in our American mythology. Our cherished myth deals with the powers which conquered a wilderness, the courage, determination, alertness, and skill which moved forward with the frontier. The historical personages of Daniel Boone, Johnny Appleseed, David Crockett, and Jim Bridger attracted a mythology which lifted exceptional achievement to superhuman achievement. The intrepid vigor of lumbermen, rivermen, and railroad pioneers created mythical figures like Paul Bunyan, Mike Fink, and John Henry.

It is true that we do not accept into full belief the myths about a Davy Crockett or a Paul Bunyan. But even in our rationalistic days we cherish and maintain our mythology. It is important to our national pride to nurture a mythology of superhuman accomplishment. We are saying to ourselves that the specific myth may be a gross and humorous caricature of the truth, but that it rests upon a basis of truth. That truth, we say, is that Americans under conditions of abnormal stress are capable of abnormal accomplishment. We can still achieve greatly, because the very great is in our blood. In that sense it may be said that we do "believe," because we hold more closely to our hearts the mythology of a gay

[7] For Hem-Iunu, see Smith, W. S., *A history of Egyptian sculpture and painting in the Old Kingdom*, 303 f, 2nd ed., Oxford Univ. Press, 1949. For Montu-em-het, see Brunton, Winifred, *Great ones of ancient Egypt*, 33, Scribner's, 1930. For the general problem, see Scharff, A., in *Jour. Egyptian Archaeology* **26**: 41–50, 1940.

and courageous skill in the face of obstacles. This can be more real to us than mere recorded fact, which might contain the cruel, the selfish, and the tawdry.

If we moderns can understand how a dogmatic truth may bind together a nation more firmly and more confidently than the mundane facts of everyday existence, then we can transfer that understanding back to the royal myth of ancient Egypt. In that culture the insistent presence and activity of the gods were accepted belief, so that men were able to give themselves up in an eagerness of devoted faith. The eyes that saw and the ears that heard accepted what was before them through the all-embracing and comforting certainty that the gods were still acting generously for the welfare of Egypt. What men saw became greater than the mere evidence of the eyes.

CHŌSEN MONDAI: THE KOREAN PROBLEM IN MEIJI JAPAN

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Chōsen Mondai (The Korean Problem) exercised Japanese minds and emotions through the whole of modern Japan's formative period, from 1868 to 1910. One need only read headlines at random in the thousands of Meiji era Japanese newspapers preserved at Tokyo University[1] to realize this, or take note of the hundreds of entries in Professor Sakurai Yoshiyuki's bibliography of books on Korea published in Meiji times.[2] And while the main chain of events, from the Korean refusal to recognize the new Japanese government (1868), through treaties, intrigues, riots, murders, and two wars, to protectorate and finally annexation of Korea by Japan (1910), has received considerable attention in our literature on the Far East, it becomes only too clear from a review of interpretative studies of these events that the "Korean Problem" for Far Eastern scholarship is far from resolved.[3] There are many questions, some of which run very deep, even to the matter of the worth of modern civilization, at least its worth versus its perils to a small state in a key area of the world. But most of these questions can be highlighted by a consideration of the Japanese role in Korea, and indeed it is in consideration of this role of Japan that the divergence of interpretation has come.

Roughly speaking the Japanese course toward assumption of control over Korea has been interpreted as made necessary or even desirable by Chinese and Korean backwardness, particularly by those who see a tendency toward progress in modern civilization; but it has also, with equal persuasiveness, been interpreted as scheming and vicious, especially by those who find much to be said for the old Confucianist order in eastern Asia. The following quotations will illustrate the point: Seiji Hishida (1905), "It was the policy of the [Japanese] imperial government, whose objectives were commercial and not territorial, to secure the perfect independence of the Hermit Nation, and to lead it into the light of modern civilization."[4] W. E. Griffis (1910), speaking from "forty five years of experience with and study of the Japanese," said that "Japan attempted to redeem Chosen from medievalism . . . , to coax her into modern national life," and he credited Japan with bringing education, public hygiene, model farms, a civil service, fertilizer, and the gold standard to Korea.[5] G. Trumbull Ladd (1912) entitled an article in the *Yale Review,* "The Annexation of Korea: An Essay in 'Benevolent Assimilation.'"[6] And from the long view and a thorough search of U. S. State Department and other Western documents Payson J. Treat concluded in the 1930's that "irrespective of what individual Japanese might have thought or said, Japan wanted Korea to be independent and progressive." It was because of "ruthless destruction of this reform movement" by the Chinese, whose Korea policy was implemented by Li Hung-chang and Yuan Shih-k'ai, that "Korea sank into an abyss of misgovernment and incompetence."[7]

[1] Files of all major and many obscure Meiji period newspapers are housed in Tokyo University's Meiji Shimbun Bunko. Articles from many of them have been reprinted in Nakayama Yasumasa (ed.), *Shimbun shūsei Meiji hennenshi* (History of the Meiji era by newspapers), 15 v., Tokyo, Rinsensha, 1934–1936.

[2] Sakurai Yoshiyuki, *Meiji nenkan Chōsen kenkyū bunken shi* (Bibliography of Meiji period studies of Korea), Seoul, Shomotsudōkōkai, 1941. Sakurai discusses Japanese "consciousness" of Korea in the Meiji period as revealed in publications by individuals, private organizations, and government agencies in an article Meiji ki ni okeru taikan ishiki no ichi kosatsu (A consideration of consciousness toward Korea in Meiji times), *Chōsen Gakkai Hō* **21**: 4–5, 1954.

[3] See Eckel, Paul, *The Far East since 1500,* 270, New York, Harcourt, Brace and Co., 1948, for a text book writer's lament on the difficulties of interpretation surrounding the problem of Korea. Frank Williston points to a need for American reexamination of the Korean question in his Reflections on American-Korean relations, *Korean Review* **1**: 1–10, 1948.

[4] Hishida, Seiji G., *The international position of Japan as a great power,* 164, New York, Columbia Univ. Press, 1905. Hishida's work was done at Columbia under John Bassett Moore.

[5] Griffis, W. E., Japan's absorption of Korea, *North American Review* **192**: 516, 525–526, 1910.

[6] Ladd, G. Trumbull, The annexation of Korea: an essay in benevolent assimilation, *Yale Review,* n. s., **1**: 639–656, 1912.

[7] Treat, Payson J., China and Korea, 1885–1895, *Political Science Quart.* **49**: 514, 542–543, 1934. See also Treat's *Diplomatic relations between the United States*

Meanwhile, Chinese scholars were beginning to search Chinese records for information on the subject. In 1933 and 1935 respectively T. F. Tsiang [8] and T. C. Lin published studies which probed Chinese documents and showed that indeed there was truth in the Chinese claim that they had sought to protect Korea from foreign encroachment and to uphold an ancient and honorable Sino-Korean relationship "fundamentally similar," as Lin put it, "to that of the British Self-governing Dominions to the British Crown at present [though] alien then to the Western juridicial concept," with Korea recognizing the overlordship of China, but "singularly free in her internal administration and external relations." [9]

M. F. Nelson in his *Korea and the Old Orders in Eastern Asia* (1946) portrays this Sino-Korean relationship brilliantly, with sensitivity and appreciation, taking Westerners to task for their bland and blind assumption of the universal application of Western international concepts, which precluded their understanding it. And he leaves us with the picture of a scheming Japan, temporarily utilizing Western norms and techniques to seize Korea, as a first step in the building of a new East Asian order with Japan as the center, but lacking the ethical basis of the former Chinese system.[10]

Other studies, a number emphasizing Korean-American Relations and an important collection of Russian documents, have contributed to our understanding of the subject,[11] but the purpose of Japan —what "she" intended to do with, in, or for Korea—remains unclear. All of these studies, however, leave unexplored a veritable treasury of Japanese materials, some of which were used by Japanese scholars in circumspect fashion before the war, but which only in recent postwar years have become available in the full sense. These include Japanese foreign office records, a grand assortment of memoirs, papers, and biographies of participants in the events of the period, Diet records, the gratifyingly full newspaper coverage mentioned above, and certain extremely important Japanese secondary works.[12] It has been the author's privilege to work through many of these materials—with *Chōsen Mondai* in mind,[13] and in this article it is his purpose to propose and illustrate an approach to Japan's role in Korea which may help toward a refinement of our understanding of it.

It seems of first importance to emphasize at the outset that the use of the terms "Japan" and "her" can be misleading through much of the period of *Chōsen Mondai,* implying as they do a single, clearcut "national" Japanese approach. It is true that the Japanese did eventually reach a sort of mono-mindedness on Korea, but this came only

and Japan, 1853–1895, 2 v., especially chaps. 28, 40, Stanford, Stanford Univ. Press, 1932; and his *Diplomatic relations between the United States and Japan, 1895–1905,* especially pp. 275–277, Stanford, Stanford Univ. Press, 1938.

[8] Tsiang, T. F., Sino-Japanese diplomatic relations, 1870–1894, *The Chinese Social and Political Science Review* **17**: 1–106, 1933–1934.

[9] Lin, T. C., Li Hung-chang: his Korea policies, 1870–1885, *The Chinese Social and Political Science Review* **19**: 203–233, especially 203, 1935–1936.

[10] Nelson, M. F., *Korea and the old orders in eastern Asia,* especially 216–220, 296–297, Baton Rouge, Louisiana State Univ. Press, 1946.

[11] For example, Harrington, F. H. in his use of the H. N. Allen papers in his *God, Mammon, and the Japanese,* Madison, Univ. of Wisconsin Press, 1944; the George McCune document collection, part of which has been published in McCune, George M. and John A. Harrison (eds.), *Korean-American relations,* Berkeley, Univ. of Calif. Press, 1951; Pollard, R. T., American relations with Korea, 1882–1895, *Chinese Social and Political Science Review* **16**: 425–471, 1932–1933; Noble, H. J., The United States and Sino-Korean relations, *Pacific Hist. Review* **2**: 292–304, 1933; Jones, F. C., Foreign diplomacy in Korea, Harvard Univ. Ph.D. diss., 1936; Battistini, Lawrence H., The Korean problem in the nineteenth century, *Monumenta Nipponica* **8**: 46–66, 1952; Krasny Archiv, Russian documents relating to the Sino-Japanese war, 1894–1895, *Chinese Social and Political Science Review* **17**: 480–515, 632–670, 1933–1934; First steps of Russian imperialism in the Far East, 1888–1903, *ibid.* **18**: 236–281, 1934–1935; On the eve of the Russo-Japanese war, *ibid.* **18**: 572–594, 1934–1935; **19**: 125–139, 234–267, 1935–1936.

[12] Principal examples of such secondary literature include the careful scholarly work of Tabohashi Kiyoshi, *Kindai Nissen kankei no kenkyū* (Study of modern Japanese-Korean relations), 2 v., Seoul, Chōsen Sotokufu Chūsūin, 1940; *Nisshin seneki gaikō shi no kenkyū* (Study of the diplomacy of the Sino-Japanese war), Tokyo, Tokyo Shoin Co., 1951, and others; and the flagrantly biased but remarkably detailed and revealing publications of the Kokuryūkai (Black Dragon Society): Kuzū Yoshihisa, *Nikkan gappō hishi* (Secret history of the merger of Japan and Korea), 2 v., Tokyo, Kokuryūkai, 1936; Kuzū Yoshihisa, Nisshi kōshō gaishi (History of Sino-Japanese negotiations), 2 v., Tokyo, Kokuryūkai, 1938–1939, and others.

[13] The author originally undertook research on this subject in 1952 under a summer research grant from the Social Science Research Council and the University of Pennsylvania. Then a Fulbright research grant plus supplemental aid from the American Philosophical Society enabled him to continue his research in Japan in 1954. He expects to present his results more fully in a monograph tentatively entitled "The Japanese seizure of Korea, 1868–1910."

as the compromise of the years. Behind it lay more than three decades of kicking around in Japan this football labeled "Korean problem," and it becomes clear, when we range the personalities who turned their attention seriously and actively to Korean affairs—from the liberal educator, Fukuzawa Yukichi through Itō Hirobumi to Black Dragon Chieftain Uchida Ryōhei, that they represent an extremely wide range of political colorings. While recognizing that in political hue even so many as two individuals are rarely exactly alike, I would nevertheless divide these people into three groups, which, from their respective positions in Japanese politics and their aims concerning Korea, we may designate in clumsy terminology as follows: Liberals, Realists, Reactionaries. The groupings and the names may be artificial, but however designated, they represent three different starting points in the Japanese approach to Korea—ideologically and philosophically far apart, like three different springs in the mountains. This is important, but more important—in understanding what happened as opposed to what was supposed to happen—is the way in which in the long course of action and interaction the three streams merged into one, fused as it were into the flood that engulfed Korea.

The first group, the Liberals, were those who desired and worked for an independent, progressive, parliamentary Japan, for the best blessings Western civilization seemed to hold for an awakened Oriental country that had slept too long. The Liberals would include the party men, from regulars like Itagaki Taisuke and Ozaki Yukio to rebels like Ōi Kentaro, but I shall consider Fukuzawa Yukichi as the model of the group, for his connection with the Korean affair is very clear, and being both outspoken himself and without political office or ambitions, he, unlike Itagaki or Ozaki, need not be suspected of formulating Korean policies to serve his own political career in Japan. And though Ōi would certainly serve as an excellent example of liberal thought and perhaps *the* leader of liberal action on Korea, still Fukuzawa seems to have a fuller awareness of what would constitute basic underpinnings of liberalism and so seems more properly the "model" of the Liberals.[14]

What was the Liberal creed toward Korea? In a word it was "Help Korea," help her from the old erroneous way of Confucianism, isolation, misgovernment into the light of modern civilization, toward independence and progress. How should this be done? In his newspaper, *Jiji Shimpo*, Fukuzawa urged reliance on "modern civilized philosophy" rather than force, on the extension of "gakumon no bunken" (the civil power of learning) to Korea. This meant that Korean students should receive a modern progressive education, and as early as 1881 Fukuzawa had some of them living in his own house. They reminded him, he said, of himself as he had been as a student in the United States. He urged that Japan must be prepared to spend money on the progress of Korean civilization, to send advisers to Korea, to give aid to progressive young Koreans, and he set out to do what he could in his private capacity to help the cause. This led him into an extremely close relationship with Kim Ok-kiun and other Korean progressives, and into a network of intrigue, for, impatient at finding their reform program thwarted by the Min faction, the Tae-wongun faction, and the Chinese in Korea, the "progressives" found it necessary to become revolutionaries, plotting with their Japanese friends to overthrow the old order. Fukuzawa was certainly involved in the planning of the abortive *coup d'état* of 1884. He helped its ringleaders, Kim and Pak Young-hyo, in efforts to enlist the aid of Gotō Shōjirō and other Liberal Party members, and after the attempt Kim, now in hiding, "again lived at Fukuzawa's house." [15]

[14] In choosing a "model" for each group the author is not seeking merely a member of the group, but a leading, sensitive, competent member—a man or the man who represents the group's basic approach at its best. On this basis Itagaki and Ozaki do not measure up as well as Fukuzawa. E.g. Roggendorf thinks Itagaki a "mere opportunist" (though Ike finds him motivated by "genuine democratic principles"). See Joseph Roggendorf, review of *The beginnings of political democracy in Japan* by Nobutaka Ike, *Monumenta Nipponica* **8**: 441, 1952. Ozaki's own words may be taken to indicate the use of the Korean problem merely as a political weapon against Itō's leadership, Ozaki Yukio, *Gakudō kaikoroku* (Memoirs of Ozaki Yukio) **1**: 214–216 Tokyo, Yūkeisha, 1951. For a penetrating search for the roots of Fukuzawa's thought see Maruyama Masao, Fukuzawa Yukichi no tetsugaku (The philosophy of Fukuzawa Yukichi), *Kokka Gakkai Zasshi* **61**: 129–163, 1947. If Maruyama's findings even approximate the truth, Fukuzawa emerges as one of the truly profound and sensitive liberal thinkers.

[15] Ishikawa Mikiakira, *Fukuzawa Yukichi den* (Biography of Fukuzawa Yukichi) **3**: 277–278, 289, 294–295, 296–297, 312, 340–341, 417, Tokyo, Iwanami Shoten, 1932. Tabohashi, *Kindai Nissen* **1**: 909, calls Fukuzawa a leader of the Korean "new man"; see also Tabohashi, *Nisshin*, 3; *Jiji Shimpo*, Aug. 30, 1910. *Jiji Shimpo* which was formerly Fukuzawa's newspaper, beginning Aug. 30, 1910, in commemoration of Korean annexation,

Even the failure of the *coup* did not dampen the enthusiasm of the Japanese friends of Korean progress, and many of them, for example Inoue Kakugoro, who "stayed for three years in Fukuzawa's house and was much influenced by his discussions," [16] Kobayashi Kazuo, secretary of the Liberal Party,[17] the aforementioned Ōi Kentaro, who was an avid student of French law and philosophy, continued to scheme, raise money, and collect weapons "for Korea." In 1885 they actually put in motion from Osaka a "help Korea" expedition of thirty or forty people, the advance guard of which got as far as Nagasaki. It is very difficult to estimate the motives of the various adventurous spirits who joined the band. Some were probably self-seekers, the disappearance of some of the funds lending credence to this view, but the idealism of the leaders held up as they were hailed to court and jail by Japanese authorities. At his trial Ōi described the purpose of the expedition as "not to accuse the Koreans of impoliteness or to invade them," but "to help them from difficulties" and to help the Korean independence party "attain independence" and "give safety and happiness to the Korean people." Ōi expected that he might not be believed. But who would question the motives of the young school teacher from Okayama prefecture who as a "nineteen-year-old virgin" had joined the cause. Fukuzawa himself, narrowly escaping prosecution, persisted in helping Kim and his family, and he regarded the Japanese government's cool attitude toward Kim as "atrocious." [18]

The ideological theme of this Osaka incident is perhaps best expressed in a "Proclamation of Independence for Korea" which was drawn up by the leaders of the band. It urged that the "great principle of freedom cannot fail" and referred to the "beautiful story" of "thirteen states [American] against England," and the French assistance [to America]. [19]

We catch a parting glimpse of these sterling advocates of Korean progress in 1894 at a graveyard in Aoyama after Kim Ok-kiun's assassination in Shanghai on orders of the Korean court. Immediately after the assassination Ōi, Inoue, etc., organized a Society of the Friends of Mr. Kim and sent a representative to Shanghai to obtain his body. Failing in that, they reverently buried some of his hair,[20] even as his corpse, returned to Korea, was being hacked to pieces by his unenlightened countrymen.[21] Fukuzawa praised Kim in an editorial.[22]

Nevertheless, it is clear that the passage of time, the realities of operation "Help Korea" and perhaps the corrosive influence of other groups at work on the Korean problem brought Fukuzawa to accept and even to endorse ideas and actions that were leading to something quite different from the independent, progressive Korea originally envisioned by the Liberal group. First we see hints of his becoming dissatisfied with some of his Korean friends, other than Kim; he once described Kim as "the only one among the Koreans to be relied on." [23] And no wonder, for some of them seemed to lose their revolutionary ardor; living in Japan at the expense of their friends, "they were not shy about throwing money around for pleasure as well as for daily livelihood." [24] As the Sino-Japanese war drew to a close and

published serially a "previously unpublished" memoir of Fukuzawa's on his friendship and aid to Kim, etc.

[16] *Jiji Shimpo*, Aug. 27, 1910 (article written by Inoue Kakugoro); *Fukuzawa den* **3**: 345–369; Ishikawa Ryoi-hi (ed.), *Jiyūtō Ōsaka jiken* (The Liberal Party's Osaka incident), 12–14, Tokyo, Jiyūtō Ōsaka Jiken Shuppankyoku, 1933.

[17] Fukuzawa seems to have recommended Kim to Gotō Shōjirō of the Liberal Party for a loan. Gotō put him in touch with Kobayashi, who knew French, had friends at the French legation, and tried to get the money there. Tabohashi, *Nisshin*, 4; *Jiyūtō Ōsaka jiken*, 12–27.

[18] Tabohashi, *Nisshin* 5, **7**, 8–9; Jansen, Marius, Ōi Kentaro, *Far Eastern Quarterly* **11**: 307, 1952; Hirano Yoshitaro, *Bajō Ōi Kentaro den* (Biography of Ōi Kentaro, pseud. Bajō), chaps. 1, 2, 5, esp. pp. 148–152, Tokyo, Ōi Bajō Den Hensanbu, 1938; *Fukuzawa den* **3**: 363–369; Oka Yoshitake, Jiyūtō saha to nashiyonarizumu, Ōi Kentaro no baai (The left wing of the Liberal party and nationalism, case of Ōi Kentaro), *Shakai Gaku Hyōron*, 11, May, 1951; *Jiyūtō Osaka-jiken* (entire) is a full though rambling description of the incident.

[19] *Bajō Ōi*, 94. A contributor to the collection of memoirs and papers regarding the affair carries on the idea to compare Ōi and company with Lafayette in the American or Byron in the Greek fight for freedom, *Jiyūtō Ōsaka jiken*, 2–3.

[20] Tabohashi, *Nisshin*, 38; Japanese Foreign Office, History of relations between Korea and Japan, Japanese Ministry of Foreign Affairs Archives (Library of Congress microfilm) **SP 5**: 75, confidential, 1894. Hereafter documents in this vast collection of unpublished documents from the Japanese Ministry of Foreign Affairs, which was microfilmed for the Library of Congress, will be cited as "Japanese Foreign Office (microfilm)" with series number noted in bold face, pagination (order of microfilming within series) in regular face.

[21] Allen to Gresham, Apr. 17, 1894, U. S. Dept. of State, Diplomatic despatches, Korea, No. 554; Japanese Foreign Office (microfilm) **SP 5**: 74–76.

[22] *Fukuzawa den* **3**: 386.

[23] *Ibid.*, 399.

[24] Tabohashi, *Nisshin*, 9.

Japanese control over Korea grew tighter, Fukuzawa may be seen refuting arguments that "Japanese policy was restricting the Korean government even more than had the Chinese."

"But," he said, "Japan is a doctor, responsible as a teacher of civilization. Korea is like a sick person whose limbs are paralysed. Japanese interference in Korea should not be made in a retiring manner, but strongly and swiftly to bring Korean entrance into civilization." [25]

Fukuzawa did not live to see the final steps in the Japanese seizure of Korea, the protectorate, the forced abdication and the annexation, but there is little doubt that he would have approved of them as "necessary." [26] The Tokyo Metropolitan police kept close tabs on political groups of Fukuzawa-ish hue in the 1905–1910 period. A few of them are reported as "disappointed" when they heard that the Korean reformer, Pak, once the bosom friend of Kim and Fukuzawa, had turned against the Japanese and had been arrested in Seoul.[27] But all in all the police reports to the Foreign Minister show the Liberals to be supporting government policy.[28]

What was "government policy?" To find it we must turn to the "Realists," the leaders of the Meiji government, such figures as Itō Hirobumi, Inoue Kaoru, Mutsu Munemitsu, Yamagata Aritomo, and the host of lesser figures who served them as diplomats in Korea, China, and around the world, and in the Japanese military establishment. It was they who charted the course and set into execution the modernization program in Japan. In so doing they put sentimental attachments for old ways and old virtues out of mind; they faced the future with stern realism, determined to do what was necessary to build Japan into a full strength Western-style nation, free of unequal treaties, safe from foreseeable future dangers, fully able to compete amongst the Powers. They set out in pursuit of objectives in Korea, as in Japan, which may be epitomized in the words "Reform and Security." Like the Liberals they wanted to help Korea toward reform and progress, toward *kaikoku* (opening closed country and closed minds), toward sound government, solvency, and independence,[29] partly for "Civilization's" sake and for the good of the Koreans, but mostly because it seemed essential to the security of Japan. They knew Japan's international position to be precarious, and it was axiomatic to them that serious danger lurked in backward, unsettled, unfriendly, unpredictable conditions in Korea. But they were not rash, not anxious to spend money and men in foolish or unnecessary enterprises. They would do only what "had to be done." Itō, the soul of caution, stands as the model and most powerful figure of the group. All were not as cautious as he, but as a group they worked at the problem carefully, prepared for "realistic" compromises, weighing alternative plans

[25] *Fukuzawa den* **3**: 440–441 (date *ca.* 1895). It is interesting that Inoue Kaoru, representing the government in Seoul, used the same doctor-sick man thesis in reporting to Foreign Minister Mutsu, Nov. 4, 1894, Japanese Foreign Office (microfilm) **MT 1615**: 974.

[26] Fukuzawa died on Feb. 3, 1901. Shortly before his death he expressed his feelings in general terms, "I am very satisfied with the development of Japan up to now." Rekishi Gaku Kenkyūkai (ed.), *Nihon shakai no shiteki kyūmei* (Historical studies of Japanese society) 211, Tokyo, Iwanami Shoten, 1949.

[27] Itō to Saionji, July 22, 1907, Japanese Foreign Office (microfilm) **MT 2419**: 318–319; Chief General Staff to Commanding General in Korea, July 24, 1907, *ibid.*, 431; Metropolitan Police to Foreign Minister, Aug. 14, 1907, *ibid.*, 653–655; Hasegawa, Japanese Commander in Korea to Foreign Minister, Sept. 3, 1907, *ibid.*, 1126–1131.

[28] Metropolitan Police to Foreign Minister, Aug. 14, 1907, Japanese Foreign Office (microfilm) **MT 2419**: 653–655. This report is especially interesting for it refers to the Nichi Kan Doshi Kai (Japan Korea Friendship Society), composed of Japanese friends of Pak. See also Metro. Police to For. Min., July 26, 1907, *ibid.*, 515–516 (re Daido Club, Diet members of Ozaki hue); Metro. Police to Foreign Min., July 26, 1907, *ibid.*, 541–542; July 28, 1907 *ibid.*, 578–580 (these are re Shimpoto and Okuma); Metro. Police to For. Min., July 26, 1907, *ibid.*, 548 (re Yukōkai); Chiba governor to For. Min., July 27, 1907, *ibid.*, 565–567 (re journalists of Chiba); Metro. Police to For. Min., July 30, 1907, *ibid.*, 599 (re Eto Shinsaku and Kensei Honto). The only resolution opposing the government action (new convention) came from "two or three" socialists, Kōtoku, etc. See Metro. Police to For. Min., July 23, 1907, *ibid.*, 362–363; July 27, 1907, *ibid.*, 513–514. Itagaki, Okuma, and Inoue Kakugoro all voiced approval of annexation in *Jiji Shimpo*, Aug. 27, 1910.

[29] For definite statements of these aims, including Korean independence, even amidst Sino-Japanese war fever, see Mutsu to Itō, June 27, 1894, Japanese Foreign Office (microfilm) **MT 1615**: 58–62; Mutsu to Itō, Aug. 7, 1894, Japanese Foreign Office (microfilm) **MT 1615**: 488–491; Cabinet decision, Aug. 8, 1894, *ibid.*, 495. If these records had been addressed to the outside world they might be dismissed as propaganda, but they are not; they are inside Cabinet shoptalk.

at every critical juncture,[30] and always considering the attitudes of foreign nations.[31]

Their records reveal a great variety of frustrations from small matters to large: e.g., the frantic efforts of the Korean government to ship Minister Hanabusa's furniture after him when he returned to Tokyo on a visit in 1878, the Korean refusal to follow Inoue's urging and accept an American treaty in 1880, on the grounds that the American letter was improperly addressed—a refusal that was, in the words of the Japanese Foreign Office's confidential memo to itself, "extremely against our advice," the failure of efforts to reform the Korean coinage (1891–1893) in spite of credits granted by the Yokohama Specie Bank and the efforts of a Japanese mint director—(a two-year Sino-Korean argument over whether the character *Dai* [great] should be used on the coins halted operations).[32] During these years to 1894 Itō and his fellow policy makers, of course, observed the Chinese hand working through and with Korean court reactionaries to block their efforts to promote reform and independence in Korea, but they also found that, without military measures, which they were anxious to avoid, they could only retreat from their objectives time and again. In so doing they set a "realistic" but none the less unseemly pattern of abandonings of Korean reform and reformers: as in requiring Minister Takezoe in Seoul to turn his back on the rebel reformers of 1884, after he had, without instructions from his government, encouraged them;[33] as in taking an unsympathetic attitude to Korean reformists who had come as political exiles to Japan, easing them out of the country[34] (Kim Ok-kiun, himself, being sent to the Bonins and then to Hokkaido);[35] as in hauling their Japanese friends to court;[36] as in Foreign Minister Mutsu's cold and official pronouncement (April, 1894) that the murder of Kim was "outside our authority."[37] The Emperor had proclaimed in a rescript to prefectural governors in February, 1885, "Negotiations with foreign countries are very important. The nation's national eternal great accounting interests must not be misled. Neighboring relations should be achieved in a conciliatory manner."[38] "Security" demanded caution.

But by 1894 "security" demanded more. As Japan's policy makers looked beyond China to Russia they felt a terrible pressure on them to settle the problem of Korea. Yamagata warned the Emperor in 1892 that the construction of the trans-Siberian Railroad was bringing on a crisis in the Far East for which Japan must be ready,[39] and gradually official thinking on the matter of Korean reform came to the view that reforms *must* be accomplished in Korea even if it required military interference to obtain them.[40] Itō continued cautious, but the pressure of events and

[30] Itō's interest and influence in Korean affairs was second to none. And he was determined that his cautious approach should prevail. Note his special precautions on becoming resident general to insure that he would control Japanese military as well as civilian personnel in Korea. Hiratsuka Atsushi (ed.), *Itō Hakubun hiroku* ([Hitherto] unpublished letters of Itō) No. 77, 315, Tokyo, Shunjūsha, 1929. For examples of thinking in alternatives see Japanese Foreign Office (microfilm) **SP 5**: 10; Mutsu to Itō, Aug. 16, 1894, *ibid.*, **MT 1615**: 540–557; see also *ibid.*, **SP 5**: section 4; Komatsu Midori (ed.), *Itō Kō zenshū* (Collected works of Prince Itō) 1: Bunshū section, 211, Tokyo, Itō Kō Zenshū Hankōkai, 1927.

[31] Eg. Mutsu to Ōtori, Aug. 21, 1894, Japanese Foreign Office (microfilm) **MT 1615**: 559–570 stresses "international law"; also note numerous letters, clippings, etc., revealing great concern for attitude of the Powers, especially at the most critical times, 1894 and 1907, e.g. **MT 1615**: 049–050, 046, 053, 290, 538; **MT 2419**: 107, 269, 284–288, 311–312, 337–339, 381–383, 370–371, 536–538, 585–586, 610–611, 681–682, 692–696, 794, 1236–1238.

[32] Japanese Foreign Office (microfilm) **SP 5**: 26, 31–32, 73–75. According to this Japanese Foreign Office memoir the argument about the year title was between Koreans and Chinese, as was a coincident argument as to whether the Koreans should use *Dai* (great) in Dai Chōsen. The Chinese held that this could be used only in *foreign* affairs. The Korean government made the contract with a Mr. Omiya (mint director) in 1891.

[33] Japanese Foreign Office (microfilm) **SP 5**: 47–50; *Fukuzawa den* **3**: 342–344; Kuzū, *Nisshi kōshō gaishi* **1**: 183; Tabohashi, *Nisshin*, 1–2. Takezoe would not even help the "reform party" find ship passage after the abortive coup, nor would he give them asylum at the Japanese legation.

[34] Tabohashi, *Nisshin*, 8. Pak Young-hyo, So Che-pil and So Kwang-pom went to America. Perhaps the Japanese government passed expense money to them via Fukuzawa.

[35] Japanese Foreign Office (microfilm) **SP 5**: 63–64, 75; Kuzū, *Nisshi* **1**: 218–219.

[36] Tabohashi, *Nisshin*, 8–9; *Fukuzawa den* **3**: 363–369.

[37] Tabohashi, *Nisshin*, 41.

[38] Japanese Foreign Office (microfilm) **SP 5**: 56.

[39] Kuroda Kashihiko (ed.), *Gensui Terauchi Hakushaku den* (Biography of Count Terauchi), chap. 8, 183–184, Tokyo, Gensui Terauchi Hakushaku Denki Hensho, 1920; Kuzū, *Nisshi* **1**: 206 ("devilish hand of Russia").

[40] Mutsu to Itō, June 27, 1894, Japanese Foreign Office (microfilm) **MT 1615**: 58–62; Mutsu to Ōtori, July 8, 18, 1894, *ibid.*, 181, 298. The government line newspaper *Nichi Nichi* (Tokyo) emphasized, July 20, 1894, "It [military intervention] is unavoidable. . . . There is no other purpose than to recommend internal reform to Korea."

the pressure of "bolder" (or more frightened) thinking by his subordinates pushed him ahead. Thus he approved the dispatch of a brigade to Korea on June 3, 1894, thinking in terms of two thousand men. But his Foreign Minister Mutsu and Deputy Chief of Staff Kawakami thought it necessary to send a "combined" brigade of seven to eight thousand men.[41] These it was anticipated would bring swift "reforms," but Ōtori, the Japanese Minister in Seoul, found it more expedient to rely on the powerful but entirely reactionary Tae-won-gun than on the Korean reform party to put the reform program into action.[42] Mutsu gave his consent to this, but he was taken aback shortly thereafter when Ōtori saw fit to begin disarming all Korean troops,[43] Japan's "allies." Mutsu voiced disapproval of this at an emergency cabinet meeting in Tokyo and orders were sent to Ōtori to desist. Also Ōtori soon found the Tae-won-gun impossible as a vehicle for the reform program, and was moving to re-enlist the aid of the Pak (Young-hyo) Korean reform faction, as well as returning arms to Korean soldiers, when he was recalled.[44]

Itō then sent the master diplomatist, Inoue Kaoru, to Korea to save the situation, but even he could not reconcile Korean politics and the Japanese reform program.[45] At first he tried to work through Pak's reformist faction to influence the Court and at one point he thought he had the way opened.[46] But he was soon bogged down, as he thought, for lack of funds, sending urgent pleas to Tokyo ("Now it is they [Koreans] who are pressing me for speedy realization [of funds]. I am at bay. I want an answer. Yes or no . . ." [47]), and complaining bitterly that Tokyo bankers were setting exorbitant interest rates on a prospective Korean loan ("I cannot morally allow them [Koreans] to contract a loan on such unfavorable terms . . ." [48]).

In the end Inoue gave up his effort to accomplish reforms through the reformers and began, in the words of the First Secretary of the Japanese Legation in Seoul, "caressing the King and the Court . . . Inoue's main business became transmitting money to the King and sending his relatives to Japan to study." [49] The reformers were, of course, embittered, reform made no headway, and finally Inoue had to renege on all promises of loans to the Korean Court when the Japanese Diet refused to approve a three million yen Korean loan appropriation he had demanded as minimum working capital. It was in embarrassment and failure that Inoue left Korea in September 1895.[50] And the murderous extremes which his successor, Miura Goro, then countenanced (irresponsibly, with no authorization from his superiors) [51] in a sense epitomized the utter frustration responsible Japanese policy makers had encountered in their efforts to make "reform and security" consonant with Korean "independence"—and decency. Itō apologized publicly for the complicity of "unworthy sons of Japan" in the Queen's murder plot, and Miura and others implicated in the plot were recalled to Japan to stand trial. The fact that they were not convicted, however, suggests that

[41] Kuzū, *Nisshi* **1**: 226–227.

[42] Mutsu to Ōtori, July 28, 1894, Japanese Foreign Office (microfilm) **MT 1615**: 416–418; Aug. 5, 1894, *ibid.*, 487; Aug. 21, 1894, *ibid.*, 559–566; Ōtori to Mutsu, Sept. 21, 1894, *ibid.*, 624–625.

[43] Mutsu to Itō, Aug. 7, 1894, *ibid.*, 488–494; Cabinet decision, Aug. 8, 1894, *ibid.*, 495; Mutsu to Itō, Aug. 15, 1894, *ibid.*, 528–538 (speaks of paying for Korean goods, not injuring Korean pride, etc.).

[44] Ōtori to Mutsu, Sept. 18, 1894, *ibid.*, 596–597; Sept. 21, 1894, *ibid.*, 624–625; Oct. 1, 1894, *ibid.*, 616; recall of Ōtori, *ibid.*, 672; see also Kuzū, *Nisshi* **1**: 438.

[45] Inoue's reports of the problems he faced and his efforts to solve them make interesting reading. See Japanese Foreign Office (microfilm) **MT 1615**: 974–1053, 1056–7, 1076–1126, 1242–1245 (working with Pak, need money), 1279–1301 (trying to gain prestige for King), 1480–1486 (plots of Tae-won-gun), 1415–1443, 1568–1581 (re grandson of Tae-won-gun). Most of these are dated between December 1894 and May 1895.

[46] Inoue to Mutsu, Jan. 7, 1895, Gaimushō, *Nihon gaikō bunsho* (Japanese foreign affairs documents) **28**: part 1, 377, Tokyo, Nihon Kokumu Rengō Kyōkai, 1953.

[47] Inoue to Mutsu, Jan. 11, 1895, *Ibid.*, 317; also Japanese Foreign Office (microfilm) **MT 1615**: 1260–1262 ("need five million yen or can do no more").

[48] Inoue to Mutsu, Jan. 16, 1895, *Nihon gaikō bunsho* **28** (1): 319.

[49] Japanese Foreign Office (microfilm), Sugimura diary **PVM 3**: 677, 682, 686.

[50] *Ibid.*, 686, 692.

[51] Queen Min was murdered on Oct. 8, 1895, by Japanese and Korean cutthroats who entered the palace in darkness, cut her down and burned her body in the court yard. Sugimura, Japanese legation secretary, speaks of Miura's having been visited by Japanese adventurers who protested the King's "bad attitude." There is evidence aplenty, including Miura's own admission, that he and other members of the Japanese legation, including Sugimura, knew of the plot in advance. But it is also evident from the tone and content of government dispatches to Miura and Sugimura after the incident that their superiors in Tokyo were surprised, embarrassed, and distressed. See Inoue to Sugimura, No. 356, Oct. 8, 1895, *Nihon gaikō bunsho* **28** (1): 492; Saionji to Miura, No. 353, Oct. 8, 1895, *ibid.*, 491; Japanese Foreign Office (microfilm), Sugimura diary **PVM 3**: 696; *Jiji Shimpo* (newspaper), Jan. 23, 1896; Nelson, *op. cit.*, 229.

currents were running in Japan which even Itō could not control.[52]

The trend continued the same. Itō and his fellow policy makers, just as in 1895 they found Korean independence unrealistic in terms of the larger problem of Japan's international position, so later found even the semi-protectorate and the protectorate not enough.[53] Events in Korea again and again made it "necessary" to take stronger measures in Korea than had been anticipated in Japan. The Korean King, who previously had not cooperated because of the Chinese, or the Tae-won-gun's or the Queen's influence upon him, *still* did not cooperate after all these were gone, and with his "grave offense" [54] in dispatching the secret Hague mission in 1907, an act which proved that "though Itō was faithful the King was not," it became clear that the measures taken by Japan (forced abdication, etc.) were "natural." Indeed all over the world realistic and responsible people, as distinguished from foolish idealists and special pleaders, admitted Japan's action to be proper.[55]

Itō, now Resident General (Tōkan) of Korea, tried as usual to be "peaceful and calm" [56] and realistic, but the forced abdication seemed to necessitate the disarming of all Koreans,[57] the disarming provoked riots, which in turn led Japanese forces to burn villages.[58] Itō deplored this, but it is symbolic of the whole trend of the realistic policy to find Deputy Resident General Sone, who was left in charge in Korea while Itō went to Tokyo in the summer of 1908, now pleading the necessity of sending Japanese troops across the Tumen River into Manchuria to break up Korean rebel bands.[59] Tokyo's answer was "no we shall not," [60] but one does not feel it is said with finality.

Thus we watch Liberal aspirations veering toward Realistic policy, but Realistic policy all the while moves toward something beyond its original intention. What was pulling them? First, the complications, the unexpected difficulties that cropped up in the effort to put idea or theory or policy into practice. As Mutsu told Itō in August, 1894, "Various unexpected happenings have led step by step to the present situation." [61] And second, the influence of our group three, the Reactionaries, personified in Uchida Ryōhei (the Korea specialist of the group and hence probably our best model), Tōyama Mitsuru and their Black Dragon—Black Ocean society compatriots.

The Reactionaries were boastful men, and hence their own records perhaps overestimate their importance. But even allowing this, it is clear that their influence as regards the Korean problem was great. This was not curiously enough, because of the success of their political program in Japan, for that program such as it was—and it was vague and ill defined—was foredoomed to failure. Ideologically they were the voice of the past, a past that was dead and could not be revived, the Old Eastern World, the Confucian heritage, the "Expel the Barbarian" part of the slogan *Sonnō Jōi* (Revere the Emperor; Expel the Barbarian); but *Jōi* had been dropped for realistic reasons, and the Confucian heritage was no longer adequate for modern life. So the Reactionaries were frustrated and ill-tempered. They could not restore the old, yet they could not stomach the new.

Forced by the defeat of Saigō's rebellion in

[52] Nelson, *ibid.*; *Jiji Shimpo*, Jan. 23, 1896; Tokyo *Mainichi* (newspaper), Jan. 23, 1896. After his trial Miura returned to Tokyo where he was welcomed by over 300 people but "no government officials," *Mainichi*, Jan. 26, 1896.

[53] Japanese Foreign Office (microfilm) **SP 8**: 6–11.

[54] Aoki to Hayashi, July 21, 1907, Japanese Foreign Office (microfilm) **MT 2419**: 284–285. This quotes *N. Y. Tribune*.

[55] Governor of Kanagawa to Foreign Minister, July 24, 1907, *ibid.*, **MT 2419**: 381–383. This quotes foreign residents at Yokohama. Japanese diplomats abroad sampled and reported opinions expressed the world around. E. G. Japanese Foreign Office (microfilm) **MT 2419**: 107–108, 794 (The Hague); 269, 284–285, 370–371, 692–696 (U. S.); 585–586 (London); 681–682 (Glasgow); 286–288, 311–312, 337–339 (Berlin); 381–383, 536–538, 610–611 (foreigners in Japan). All were favorable to the Japanese.

[56] Itō policy speech, May 30, 1907, Kuzū, *Gappō hishi* **1**: 262–264. See also Metropolitan Police to Foreign Minister, Sept. 6, 1907, Japanese Foreign Office (microfilm), **MT 2419**: 685–687. This report shows Itō called "weak kneed" because of this attitude. *Tokyo Asahi* (newspaper), July 11, 1907 pointed to Itō's responsibility in "doing nothing."

[57] Itō to Chinda, Deputy For. Minister, July 19, 1907 (2 letters), *op. cit.*, **MT 2419**: 240–242; Itō to Chinda, July 19, 1907, *ibid.*, 226–231; Itō to Saionji (Prime Minister), July 21, 1907, *ibid.*, 305; Chief of General Staff to Foreign Minister, July 27, 1907, *ibid.*, 925–926; Chōsen Commander in Chief to General Staff, July 31, 1907, *ibid.*, 980.

[58] Itō to Hayashi, Nov. 29, 1907, *ibid.*, 1288–1289.

[59] Sone to Foreign Minister, Mar. 2, 1908, *ibid.*, 1470–1474; Sone to Itō, Aug. 7, 1908, *ibid.*, 1912–1914; Sone to Foreign Minister, Aug. 12, 1908, *ibid.*, 1926–1927; same to same, Aug. 30, 1908, *ibid.*, 1963–1965.

[60] Itō to Sone, Aug. 8, 1908, *ibid.*, 1919–1920; Foreign Minister to Sone, Aug. 31, 1908, *ibid.*, 1966–1968.

[61] Mutsu to Itō, Aug. 16, 1894, Japanese Foreign Office (microfilm) **MT 1615**: 539–540; see also Kuzū *Nisshi* **1**: 438.

1877 to bow to Western-style progress in Japan, out of power and unwilling to participate in Western-style politics, as did the Liberals, to make their voices heard, the Reactionaries took refuge in emotion, moralizing over the "lost" samurai virtues of courage and loyalty, sentimentalizing about Asia, its countries and peoples, who they saw as being washed over by tidal waves from the West and being sold out by their own governments. Actually samurai loyalty and "Asia" were out of fashion even as ideals in a "Meiji" (enlightened) era, and yet there was a way, and the Reactionaries found it, to cloak them in respectability and to turn them into a powerful emotional lever, capable of stirring the conscience of the whole Japanese nation, a nation so recently emerged from the old Asiatic past that even the leaders of the march forward had moments of uncertainty. By presenting their ideals as essential ingredients of the imperial honor, the Reactionaries were able to turn to advantage a fundamental contradiction of New Japan. For the throne was the "banner of the new age";[62] it had been made so by Realist oligarchs who, determined to have modernization in a hurry, made practical use of it whenever necessary to stifle opposition. Even the Liberals, despite their enthusiasm for Western political ideas, and despite the fact that they were repeatedly the victims of the oligarchy's manipulation of the throne, could not bring themselves to attack it.[63] Yet the implications inherent in the imperial institution ran ultimately in the opposite direction from modernization and progress. In the last analysis the throne, with its "god-emperor," its age-old traditions and its mysterious workings, was more congenial to the spirit and purposes of the Reactionaries than to those of either Realists or Liberals, especially inasmuch as only the Reactionaries could claim to be an unblemished 100 per cent against the Western barbarian disturbers of His Majesty's peace of mind. Thus, out of government, never exposing themselves to the reality (and shame) of bargaining with Westerners across the conference table, they could speak as purists on imperial honor.

In Korean affairs they found a great opportunity, both to badger the government on imperial honor, as well as to play on the Asia theme. And the unsettled condition of that country lent itself to *samurai*, or more precisely, *rōnin*[64] tactics. The basic pattern of the Korean activity of the Reactionaries is revealed in their participation in the Tong Hak (Eastern Learning) movement, which came to assume the proportions of a full-scale rebellion by 1894. This movement was consistent with their ideological outlook, for it, like the Boxer movement in China a few years later, was a rebellion against the ruling dynasty for reactionary rather than progressive reasons. Disaffected Confucianists and anti-foreign elements (including the Tae-won-gun), building on widespread unrest among Korean farmers, gave the movement direction.[65] Uchida and fellow Japanese adventurers participated actively in it, the Japanese contingent being organized as the Ten Yu Kyō (Saving Chivalry under Heaven Society).[66] Though the rebellion was put down rather easily (prior to the outbreak of the Sino-Japanese War), its Japanese advocates may be seen a year later again in league with the Tae-won-gun, advocating the need for strong action to Minister Miura, planning and carrying out the murder of Quen Min. This likewise backfired. However, close associations continued between Koreans and Japanese who had been together in the Tong Hak ranks and a few years later the Society was "reconstituted in changed form" as the Ilchin Hoe (Japanese, Isshin Kai). Its Korean leaders were Yi Yong-ku and Song Pyong-chun and its Japanese "adviser" was Uchida Ryōhei. Yi described his basic aim as *Dai Tō Gappō* (great oriental federation),[67] which, of course, immediately brings to mind the East Asia Co-prosperity ideas which figured so prominently in the Japan dominated Far East of the World War II period.

[62] Anesaki, Masaharu, *History of Japanese religion*, 329, London, Kegan Paul, 1930.

[63] Scalapino, Robert A., *Democracy and the party movement in prewar Japan*, 165, 76, 90, Berkeley, Univ. of Calif. Press, 1953.

[64] Masterless (or lordless) samurai. These in feudal Japan constituted an ever unruly element, often seeking vengeance for a dead or wronged master and quite prepared to determine right and wrong without regard to laws or regulations.

[65] Hatada Takashi, *Chōsen shi* (History of Korea), 182, Tokyo, Iwanami Shoten, 1951.

[66] Kuzū *Nisshi* **1**: 220; *Gappō hishi* **1**: preface; Sunoo, Hag-won, A study of the development and the technique of Japanese imperialism in Korea, 1904–1910, *Korean Review* **1**: 47, note 70, 1948; Hatada, *op. cit.*, 180–185. Adachi Kenzō, a leading ultranationalist of the 1930's was one of the band, *Jiji Shimpo*, Jan. 23, 1896.

[67] Kuzū, *Gappō hishi* **1**: 41, 43–44. He explains this in Confucian terminology ("lips and teeth"), familiar to students of the Chinese dependent state system.

Typical of the implicit anti-Westernism, Yi wrote on one occasion to a Japanese friend, "I know it is Christianity which misleads the Korean people and if one goes more deeply, it is the American people who penetrated the Korean brain through Christianity."

"Great Oriental Federation" may have lain in the background but the Society's chief concern was with reaching a felicitous future relationship between Japan and Korea called simply *gappō*. This may be variously interpreted as union, merger, federation, or amalgamation. In it presumably a Korean could hardly be distinguished from a Japanese; it would be an Asiatic brotherhood like the Ilchin society itself. One need not question the depth of affection the Japanese and Korean members of the Society felt for one another, but it is interesting to note that eventually, after annexation, Uchida and Yi came to a parting of the ways, Uchida urging that the time for dissolution of the Society had come, Yi arguing that there remained much to be done to secure the happiness of twenty million Korean people. (The Society was ordered disbanded.)

At any rate Uchida and the Ilchin society played an important part in bringing about annexation. Uchida was recommended to Itō for service in Korea by a fellow clansman, and apparently off and on he was in the pay of the Resident General there. But he was far from being a loyal supporter of the Resident General. He kept secret his association with the Ilchin society and, becoming more and more dissatisfied with Itō's "indecisiveness," he began an active campaign to bring about the latter's resignation. While his Ilchin society tried to build a climate of opinion favorable to *gappō* in Korea, Uchida sent letters critical of Itō's "weak" administration to Cabinet members (e.g., Katsura) in Tokyo. And finally, after Itō's assassination at Harbin (October, 1909), Uchida and his friends found their opportunity. On December 4, 1909, Yi Yong-ku spoke out dramatically on behalf of "one million members" of the Ilchin society to petition Korean King and Japanese Resident General for *gappō*.[68]

At this Resident General Sone (Itō's successor) became suddenly ill[69] and *Jiji Shimpo* warned that "the Ilchin society does not represent the majority of the Korean people, though this newspaper has sympathy for the Society."[70] As the days passed and "our Japanese government did nothing, the comrades in Korea were disappointed," and Uchida and Song hurried to Tokyo to urge the ouster of Sone and the accomplishment of *gappō*, while Yi wrote letters to the same effect to high-placed Japanese and Koreans.[71]

In spite of the fears of Uchida that *gappō* might fail to be accomplished because of faint-hearted leadership in Japan, prospects for it were really very good. Government leaders like Katsura and especially Terauchi were much more friendly to the idea than Itō had been, and even Itō before his death had come a long way in the direction of something called *heigō*. Itō's secretary has left us a discourse on the origin and use of this term as applied to the Korean problem. It is much less romantic than *gappō*, which, the Western-minded secretary thought, "might be taken to mean a federation like Austria-Hungary." This could not be, and yet *heidon* (swallow up) was "too aggressive." *Gappei*, often used for business mergers, had too many different uses. *Heigō*, which was stronger than *gappei* and which "clearly meant that the other's territory [Korea's] would become a part of Japan" would be most satisfactory.[72]

Such subtle distinctions, however, were lost in the months following the Ilchin society proposal, as misgivings gave way to a sort of misty-eyed enthusiasm for the project, whatever its name, and by July, 1910, when annexation was actually accomplished, Liberals, Realists, and Reactionaries came at least to a meeting of minds on Korea and joined hands in self-congratulation at the moment of final success in the solution of *Chōsen Mondai*.[73]

Thus the course was run to final compromise, Japanese monomindedness on Korea, annexation. "Japan" was agreed that *gappō*, *gappei*, *heigō* or whatever it might be called was necessary, desirable, and at last timely. Yet one further question remains to be asked. What was the nature of the

[68] Information given in the preceding three paragraphs is taken from letters and notes reproduced in Kuzū, *Gappō hishi* **1**: 11, 42, 394–395, 596–610; **2**: 87–88, 92, 708–711. On the petition see also *Tokyo Mainichi*, Dec. 5, 1909.

[69] *Tokyo Mainichi*, Dec. 5, 1909.

[70] *Jiji Shimpo*, Dec. 8, 1909.

[71] Kuzū, *Gappō hishi* **2**: 429, 462–467.

[72] Statement of Mr. Kurachi Tetsukichi dated Nov. 1939, Kankoku heigō no iki satsu (Particulars on the annexation of Korea), 5, seen by the author at Japanese Foreign Office, Tokyo.

[73] *Jiji Shimpo* bordered its special annexation edition with flowers and birds, ran photographs and quotations of those who had been active *re* Korea, Aug. 27, 1910; see also *Tokyo Nichi Nichi*, Aug. 26, Aug. 30, 1910; *Tokyo Mainichi*, Aug. 23, 1910; *Tokyo Keizai Zasshi*, Aug. 27, 1910.

solution in terms of the intentions of the three broad groups who for their respective Liberal, Realistic, and Reactionary reasons had addressed themselves to the problem?

Here cross-currents are very interesting, and underscore the fact that though the three streams of approach to Korea are clear, their waters sometimes mixed with, or polluted, one another. For example, the Japanese Reactionaries could be completely opportunistic when it suited their "Great Duty." They shed (crocodile?) tears for dead Korean reformer Kim after his assassination. (But Uchida was opposed to bringing *live* Korean reformer Pak into the Ilchin society.)[74] Uchida, as has been noted, worked both for and against Itō's government in Korea, as also did others associated with him. They seem to have had even closer connections with Japanese army leaders.[75] Then the Liberals joined Reactionaries on occasion to embarrass the government, as when a Liberal party member, one Kurihara, was on hand to greet Miura's return to Tokyo;[76] they also played on the imperial honor theme when it suited them.[77] And, of course, general cross-currents between Liberals and Realists are well known (e.g., Okuma's joining the oligarchy), and indications of Fukuzawa's eventual endorsement of the government's Korean program have already been noted.

But which pattern predominated? Clearly the Liberal rationale was bankrupt (and perhaps the whole Liberal cause in Japan had gone bankrupt with it).[78] A test of this is on the question of Korean participation in the Japanese Diet, now that Korea and Japan were one. There is conspicuous silence on this matter, even among those who had led the fight for parliamentary government in Japan. Realist oligarchs performed operation Korea, but they found it "necessary" to cut much deeper than they originally intended, in fact to carve the patient so mercilessly that they could never hope to release him from the hospital. Certainly the Reactionaries contributed to this. Perhaps the best way to describe their contribution is to say that they jostled the elbows of the Realists with their "action campaign" in Korea and made them nervous with their yammerings about imperial honor. But even the Reactionaries, ill tempered as ever, were not really satisfied. Indeed they were groping toward the day when somehow they might focus their powerful emotional weapons in a last-ditch attempt to redeem Japan from alien ways and undertake the redemption of all East Asia.

Out of these diverse intents was forged Japan's solution to the Korean problem as we know it—a succession of benevolent looking Japanese generals ruling Korea in brutally repressive fashion, while mouthing reforms in wordy annual reports published in English.

[74] Kawano Hironaka, a Tōyama associate, spoke from the same platform as Ōi and other "Friends of Mr. Kim" in his commemoration, *Jiji Shimpo*, Apr. 21, 22, 23, 1894; Kawano Hironaka, Tōyama Mitsuru, et al. to Foreign Minister, July 14, 1907, Japanese Foreign Office (microfilm) **MT 2419**: 163–164; Kuzū *Nisshi* **1**: 218–220; *Gappō hishi* **1**: 96.

[75] *Ibid.*, 28, 149–152, 166.

[76] Tōyoma Mitsuru met Miura earlier at Yokohama, *Tokyo Mainichi*, Jan. 26, 1896.

[77] Ozaki, *op. cit.* **1**: 214–216.

[78] Maruyama notes that Japanese nationalism of the post Sino-Japanese war era came to have no demand for democratic rights, and suggests that dissenters took refuge in non political individualism. Rekishi Gaku Kenkyūkai, *op. cit.*, 215–216, 218.

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CORN AND THE MIDWESTERN FARMER

HENRY A. WALLACE

(*Read April 20, 1956*)

My purpose today is to trace rapidly the growth of the Midwest as influenced by Indian corn from the close of the American Revolution until 1955. At first the movement over the mountains from the Atlantic coast was slow but after a few decades a swelling tide of people began to exploit in a big way the power of a soil and climate superbly adapted to corn. Midwestern corn and the live stock products made from corn had the most profound effects on eastern United States and western Europe. No rapidly growing hinterland has ever made its economic power so widely and so beneficially felt.

The drama opens in 1783 with one hundred thousand Indians in the Midwest growing less than three hundred thousand bushels on less than fifteen thousand acres of land. Nearly all of this corn of the pre-white era had eight or ten rows of shallow, hard kernels. Indians preferred to grow this kind of corn, first, because it was early and, second, because they thought it had a superior flavor, especially when parched.

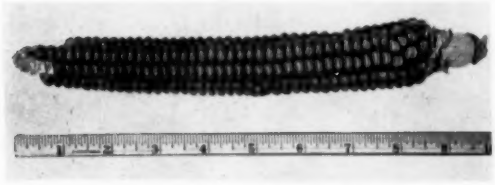


Fig. 1. A typical ear of the slender flint corn grown almost universally by the Indians in the northeast quarter of the United States. It matured early and the ears had eight or ten rows.

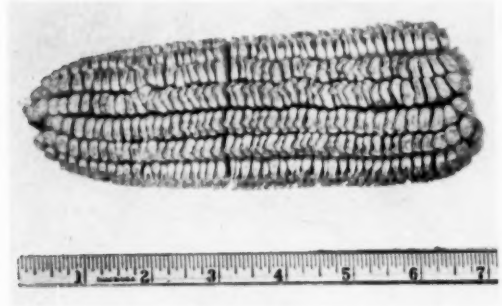


Fig. 2. Typical ear of White Gourdseed corn. This was grown especially by the Indians of Virginia and the Carolinas. Sometimes the Indians referred to this as "She" corn because of the indentations on the outer ends of the kernels. It matured late and the ears were fat with fourteen to thirty rows.

The scene suddenly shifted when white men from Virginia and the Carolinas came over the mountains bringing with them, to Tennessee, Kentucky, and southern Ohio, the corn which they had grown back home—corn with fourteen to thirty rows of deep, soft kernels. The stalks were large and the plants were slow in getting ripe. The most extreme form of this late corn was called Virginia Gourdseed because the kernels resembled in size and shape the seed of the dipper gourd. Accidental crosses of this Gourdseed type of corn were made at many times and places with the early eight-row corns. It is from this cross that nearly all of our hybrid corn of the Midwest is today descended.

For the first thirty or forty years after the American Revolution, Virginia and North Carolina were the two top corn states; and then gradually Tennessee and Kentucky replaced them and remained the two top corn states until about 1845. Cincinnati at that time was the great center of the Cornbelt and corn was marketed either as liquor floated down the rivers or driven to market on four legs. Columbus, Ohio, and Indianapolis were subsidiary centers because they were located on the national pike.

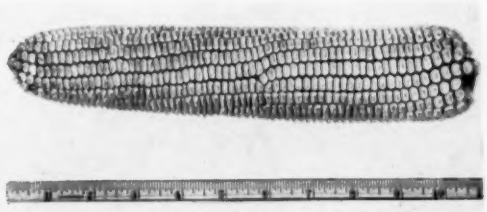


Fig. 3. Cornbelt dent ear somewhat larger than normal. Dent corn of this type was formed by the combination and recombination of the early flint corn of figure 1 with the late Gourdseed corn of figure 2.

Then came the very sudden expansion of railroads which decisively shifted the processing center of the Cornbelt away from Cincinnati toward Chicago. Those were the days when Lincoln was a railroad attorney, when politicians courted the railroads, when railroads courted the politicians and the public blessed the union with land grants as the railroads pushed ever westward to open up more and more land to corn and hogs.

In 1840 the national pike was hard surfaced only across Ohio and there were very few bridges. Facilities for the drovers were few and far between except in Ohio. There were only two hundred and thirty miles of railroads, designed to bring a certain amount of tonnage to Lake Erie and thence to the Erie Canal. There were also a number of canals in the Midwest which fed into the Great Lakes and thence into the Erie Canal. The white man had accomplished miracles in the Midwest during the sixty years prior to 1840 but they paled into insignificance when compared with the sixty years from 1840 to 1900. During this extraordinary period the population of the thirteen Midwest states increased by five times, corn production by ten times, hog numbers by four times, and railroads jumped from two

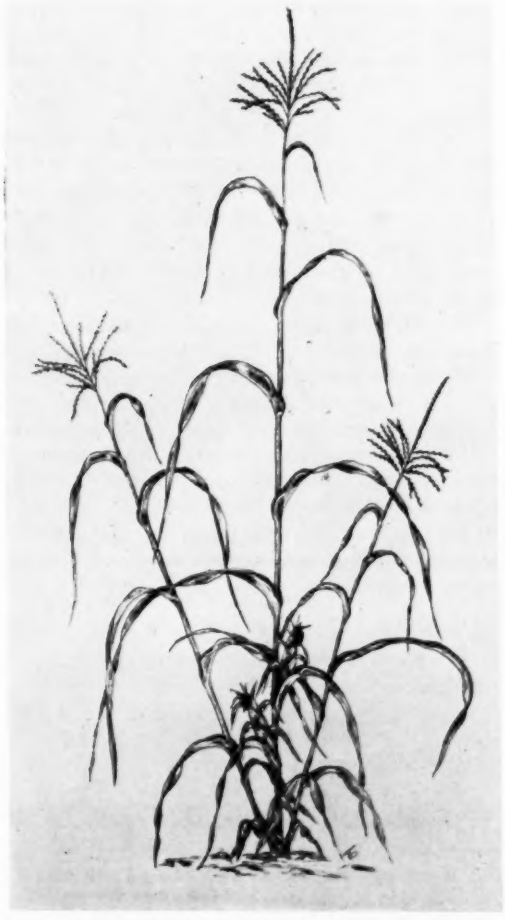


FIG. 4. Plant of flint corn, showing suckers, long slender leaves, streamers on ear shoots, long tassel branches, slender stalk, and long inter nodes.

FIG. 5. Plant of Gourdseed corn showing sturdy stalk, broad leaves, and compact tassel.

hundred and thirty miles to eighty-eight thousand miles.

From the standpoint of saving the Union the all-important growth took place between 1840 and 1860 and in particular during the decade of the fifties when railroad mileage in Ohio, Indiana, and Illinois expanded at a feverish rate. With eastern markets opening up—Illinois, Ohio, Missouri, and Indiana all suddenly passed Tennessee and Kentucky as corn states. From 1840 to 1860 corn production increased by more than two and a half times. The Civil War could not stop it. The twenty years from 1860 to 1880 saw an even more rapid increase in population, corn, hogs, and railroads than the preceding twenty years.

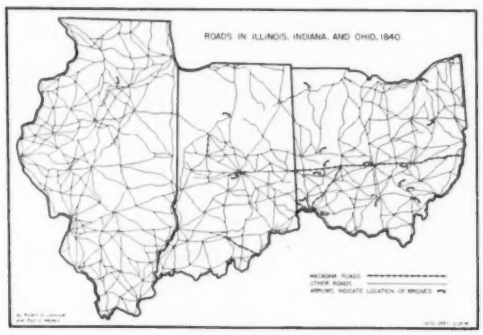
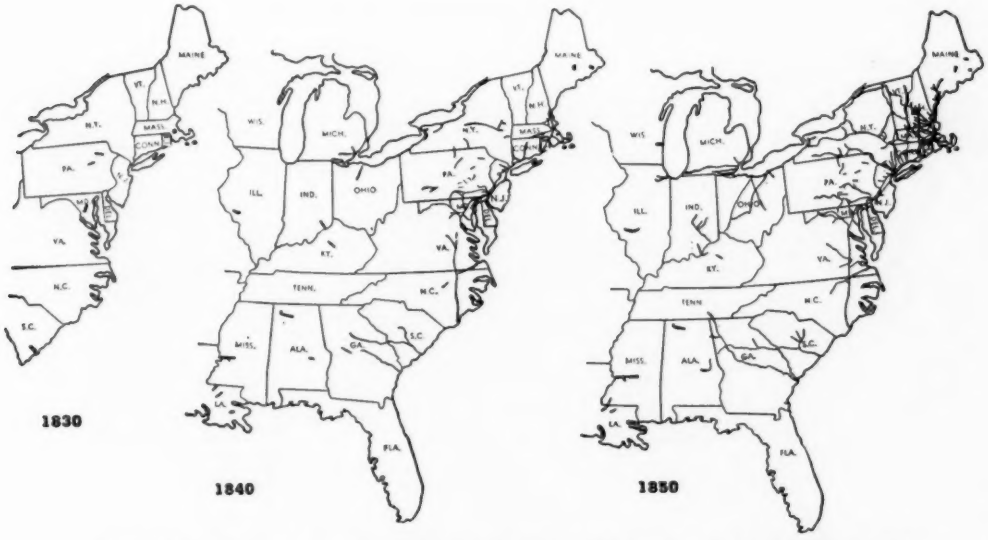


FIG. 6. Roads in the Midwest in 1840. From Paul C. Henlein, Cattle Driving from the Ohio Country, 1800–1850, *Agricultural History* **28**: 85–95, April, 1954; map prepared by R. O. Johnsrud and P. C. Henlein. Note that with two minor exceptions the National Pike was the only hard surfaced road; bridges few and far between.

After 1880 the rate of increase slowed down but the pace was still exceedingly fast. Finally by 1900 the main outlines of the Cornbelt had been defined. Just one great change remained to be made. The relatively moist weather of the eighties and nineties attracted too large an acreage of corn into Kansas. With the drier weather of the first half of the twentieth century Kansas, which had been in third place in 1899, dropped to eleventh place. Minnesota which had been in eleventh place climbed to third. The hot, dry weather which forced much of Kansas out of corn favored Minnesota. Moreover, Minnesota was



The early stages of railway development in America are shown by this set of maps. During the decade 1830-1840, the total length of completed railroad lines increased from 23 to 2,808 miles, and during the next ten years, more than 6,200 miles of railroad were opened, bringing the total network up to 9,021 miles in 1850. The most intensive growth during this period was in the Atlantic and Seaboard states. In 1850, a trip from Boston or New York to Chicago was made by rail and lake steamers or by stagecoaches, and required several days. One could travel all the way from Boston to Wilmington, North Carolina, by rail, with several changes of cars and a few ferry trips en route. During the first twenty years of railway development, covered by these maps, the population of the United States nearly doubled.

FIG. 7. Railroad maps, 1830, 1840, and 1850. From *American Railroads, their Growth and Development*, **8**, January, 1954. This and figures 8–11 reproduced by special permission of the Association of American Railroads.

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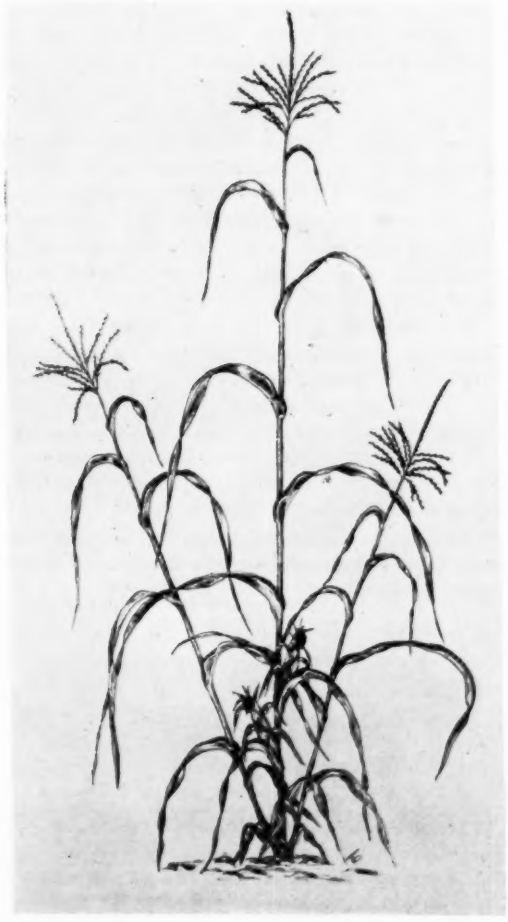

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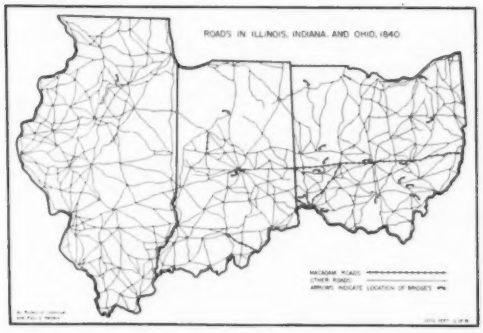

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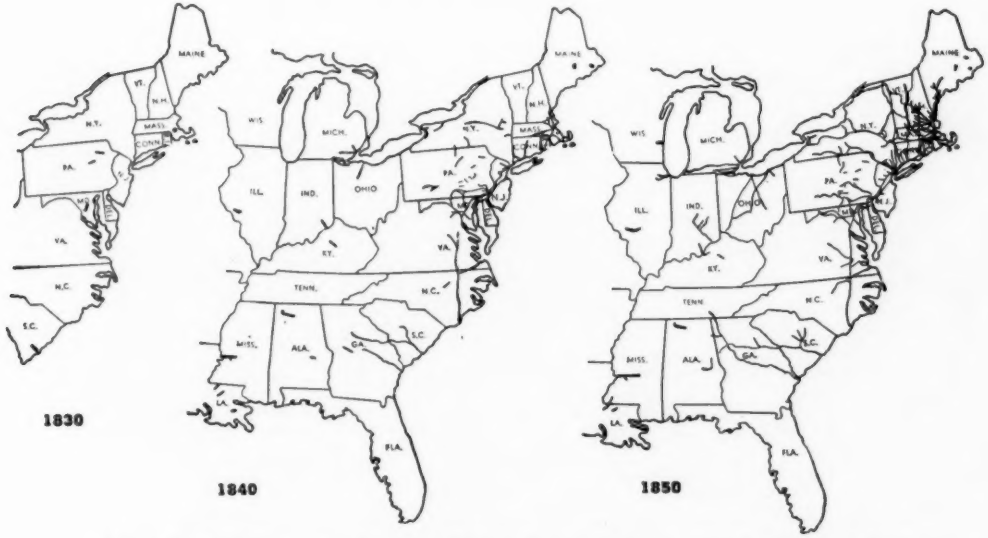

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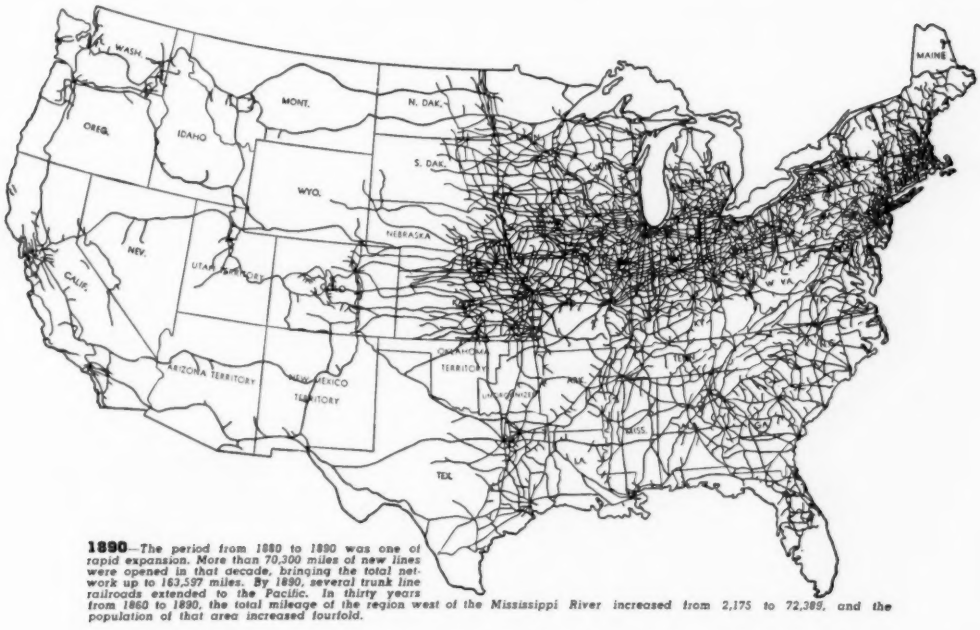
FIG. 7. Railroad maps, 1830, 1840, and 1850. From *American Railroads, their Growth and Development*, **8**, January, 1954. This and figures 8–11 reproduced by special permission of the Association of American Railroads.

1860—*This map shows the extent of railway development just prior to the Civil War. The decade 1850-1860 was a period of rapid railway expansion, characterized by the extension of many short, disjointed lines into important rail routes. This decade marked the beginning of railway development in the region west of the Mississippi River. By 1860, the "Iron Horse" had penetrated westward to the Missouri River and was beginning to make itself felt in Iowa, Arkansas, Texas, and California.*

FIG. 8. Railroad map, 1860. From *American Railroads*, 10.

1880—*In the ten-year period prior to 1880, some 40,000 miles of railroad were built, bringing the total network up to 93,267 miles. In 1880, every state and territory was provided with railway transportation. A second line of railroads to the Pacific was nearing completion, and other transcontinental railroads were under construction. Railway development was exerting a powerful influence upon immigration and agricultural and industrial growth throughout the country.*

FIG. 9. Railroad map, 1880. From *American Railroads*, 14.



1890—*The period from 1860 to 1890 was one of rapid expansion. More than 70,300 miles of new lines were opened in that decade, bringing the total network up to 163,597 miles. By 1890, several trunk line railroads extended to the Pacific. In thirty years from 1860 to 1890, the total mileage of the region west of the Mississippi River increased from 2,175 to 72,389, and the population of that area increased fourfold.*

FIG. 10. Railroad map, 1890. From *American Railroads*, 16.

1954—*Today, the American railroads embrace 222,500 miles of road and 394,600 miles of tracks. These railroads handle approximately 50 per cent of the commercial passenger and 58 per cent of the freight business of the nation, carry about 67 per cent of the United States mail and perform nearly all of the commercial express traffic of the nation. During World War II these railroads handled more than 90 per cent of the war freight and 97 per cent of the organized troop movements.*

FIG. 11. Railroad map, 1954. From *American Railroads*, 18.

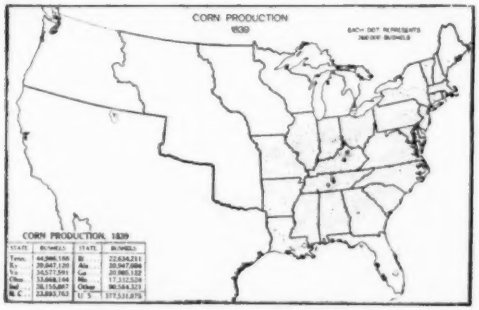


FIG. 12. Distribution of corn production by counties for the year 1839. Each dot on this map represents roughly the total amount of corn as grown by the Indians of the Cornbelt prior to 1780. During the sixty years from 1780 to 1840 the march of corn across the Midwest was fantastic in its speed. Even more fantastic was the growth in corn production from 1840 to 1880. Courtesy of the United States Department of Agriculture.

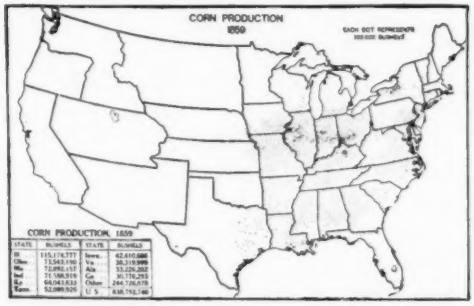


FIG. 13. Distribution of corn production by counties for the year 1859. Courtesy of the United States Department of Agriculture.

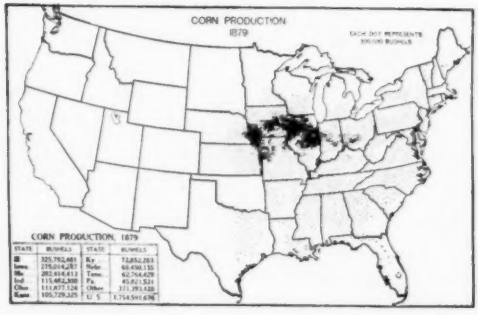


FIG. 14. Distribution of corn production by counties for the year 1879. Courtesy of the United States Department of Agriculture.

the last frontier of the Cornbelt and profited by the sudden introduction of early types of hybrid corn and new types of machinery adapted to the large farms of southwestern Minnesota.

It remains to be seen whether the periodic sun spot theory of Dr. Hurd C Willett of the Massachusetts Institute of Technology will be borne out by moister weather in Kansas during the next forty years. If so, we may see a considerable expansion of corn acreage in Kansas at the same time as the corn breeders put more emphasis on early corn for Minnesota.

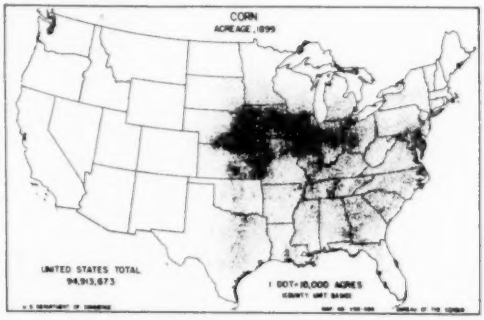


FIG. 15. Corn acreage in 1899. Note that this map is on the basis of acreage whereas those for 1839, 1859 and 1879 are on a bushel basis. Substituting the acreage basis for the bushel basis over-emphasizes corn production in the south. Courtesy of the Bureau of the Census.

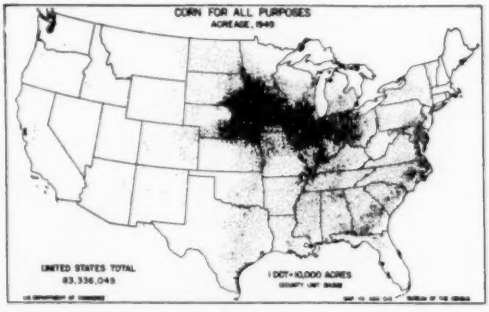


FIG. 16. Corn acreage in 1949. Note the degree to which corn acreage has been pulled out of Kansas, western Missouri, Kentucky and Tennessee while at the same time there has been an expansion in northern Iowa, southwestern Minnesota and southeastern South Dakota. This shift northward has been partly due to hybrid corn and partly to the differential impact of summers which have become somewhat drier and hotter. Courtesy of the Bureau of the Census.

Leaving the history, geography, and transportation methods of the Midwest behind us for the moment I now propose to touch very briefly on the changes in technological methods of corn production. The Indian squaw with stone and bone tools required perhaps twenty hours of woman labor to produce a bushel of corn. The white man with his horse-drawn steel plow and cultivator reduced this within a few decades to two or three hours. Thirty years ago in Iowa it still required half an hour. Today it takes six minutes. Row crop tractors and picking machines used on hybrid corn properly fertilized made all the difference. The technological revolution in the past thirty years has been just as significant as when the white man substituted horse-drawn tools for the hand labor of the Indians. But technological revolutions in their own way are expensive. Lots of labor is concealed in the manufacture of the fertilizer, the insecticides, the gasoline, and the elaborate machinery which every farmer must own if he is to produce a bushel of corn with only six minutes of his own labor. While the Iowa farmer spends less than one per cent as much labor on a bushel of corn as the Indian, the Indian had the advantage in that he was almost completely independent of the market both as a buyer and as a seller. The Iowa farmer suffers from the uncertainty of the market for his hogs, cattle, milk, chickens, and eggs. He is part of an exceedingly complex system in which there is a vast web of mutual dependence. He cannot control either the buying price of his machinery or fertilizer or the selling price of the products which represent condensed corn.

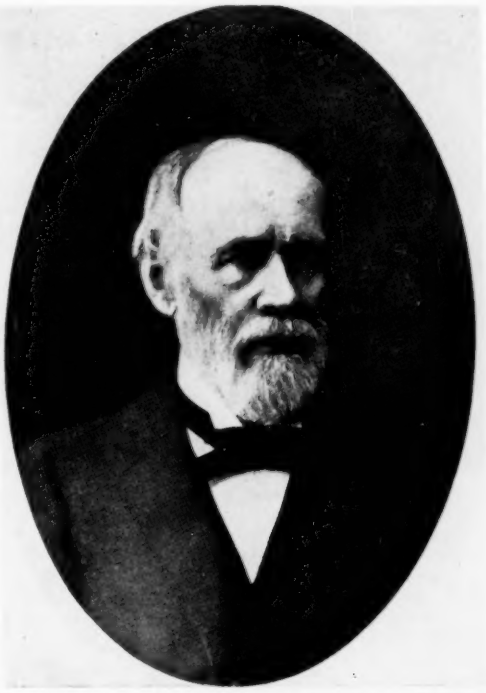


FIG. 18. Professor William James Beal of Michigan State College who was inspired by Darwin to do the first scientific crossing of corn in 1877.

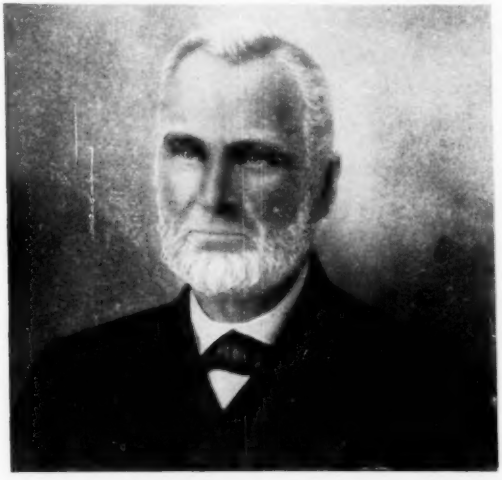


FIG. 17. Robert Reid who came from Brown County, Ohio, to Tazewell County, Illinois, in 1846 and there accidentally combined in 1847 a very late Gourdseed type of corn from Virginia with an early yellow flint. Robert and his son James by selection produced Reid Yellow Dent from this cross. From this one variety has come fully 60 per cent of the germ plasm as found in the hybrid corn as grown in the central Cornbelt in 1956.

The genius of western civilization has been to set up these great systems of mutual interdependence which involve endless division of labor, tireless scientific research, huge transportation systems, and ever enlarging markets. Corn as it has expanded in the Midwest since 1783 has played a substantial part in this modern phenomenon which looks eventually to a vast world market.

Inasmuch as I personally have been somewhat involved both as a student and a participant in certain aspects of the corn revolution having to do

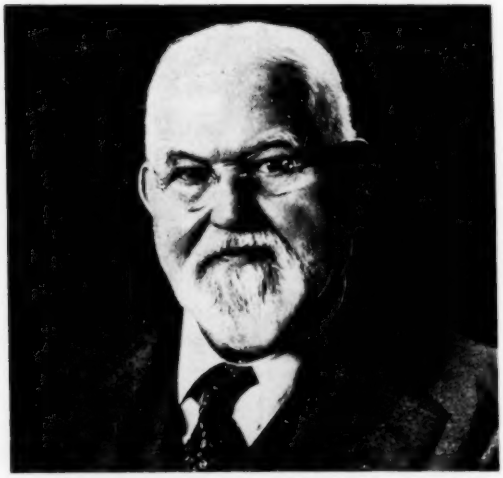


FIG. 19. Dr. George Harrison Shull, who independently but at the same time with Dr. Edward M. East began in 1905 to inbreed corn and then to cross the inbred strains. Dr. Shull did his work in a small garden at Cold Spring Harbor, Long Island, which in the year 1956 was still being used for scientific work in corn genetics. (Photo by courtesy of *Genetics*.)

FIG. 20. Small garden at Cold Spring Harbor, Long Island, where Dr. George Harrison Shull did his inbreeding work in 1905. Out of this garden and a similar small one of Dr. E. M. East in 1905 came great wealth-producing power for the future. Greater by far than the strike of a great oil field.

with genetics, I shall describe the ancestry of the corn now being grown in the Cornbelt. As I mentioned earlier the white farmers who came over the mountains from North Carolina, Virginia, and perhaps also from southeastern Pennsylvania brought with them corn which had fourteen to twenty-four or even thirty rows to the ear. The best description we have of this corn has been left us by John Lorain who lived on top of the hill in Germantown overlooking Stenton Hall of James and George Logan fame. Lorain in a letter to the Philadelphia Agricultural Society in 1812 described a corn which he called White Virginia Gourdseed which had many rows of deep kernels and which when crossed with the eight-row corn produced a sort which he said would yield one-third more to the acre. It was this cross which is now called "dent corn" but which historically might well be called the "Lorain cross" which went over the mountains to be widely grown in the Ohio Valley and the Blue Grass region

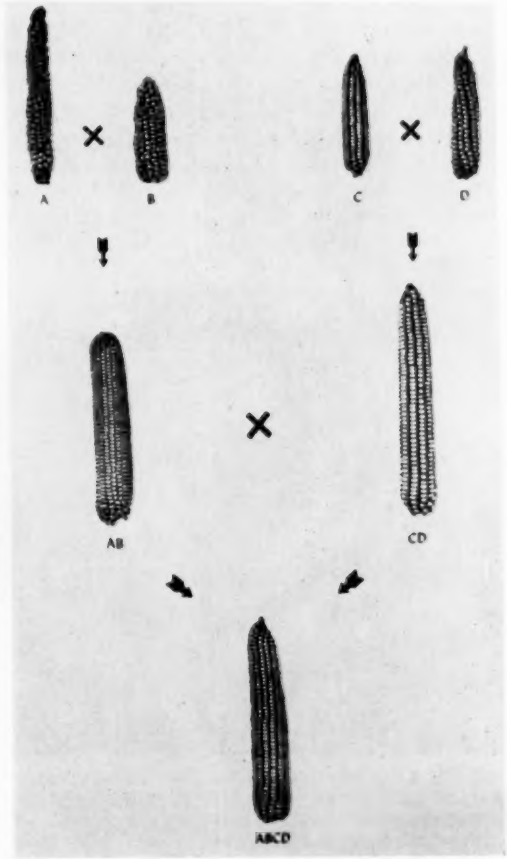


FIG. 21. Representation of the way in which four inbred strains of corn are combined in the production of a "double cross." Dr. Donald F. Jones popularized this approach to modern hybrid corn.

of Kentucky. Slowly but surely "dent corn" triumphed over the earlier, lower yielding, eight-row flint corns.

I shall cite a case history of considerable importance to the future of hybrid corn. In early 1846 Robert Reid took with him from extreme southern Ohio to central Illinois a Gourdseed kind of corn which he had obtained from a neighbor who had brought it with him from Virginia. Like all Gourdseed corn this one was late maturing and did not get ripe when planted in central Illinois in 1846. In 1847 Robert Reid planted the seed of his highly prized Virginia corn but it germinated very poorly and so he replanted it with a kind called "Little Yellow." The name "Little Yellow" in those days was widely applied to very early flint corn with eight or ten rows. In the fall of 1847 Robert Reid harvested for seed an accidental cross between the early planted Gourdseed and the late planted "Little Yellow." He had done what Lorain had recommended as the best kind of corn breeding forty years before. James Reid, the son of Robert, took his father's accidental cross and made a corn of intermediate maturity which pleased him because it was smooth and easy to husk. It is from this corn that 60

FIG. 24. A modern plant for processing hybrid seed corn in a scientific way to insure uniform size of kernels, treatment with proper fungicides, and maximum germination.

FIG. 22. A seed corn field with the tassels pulled out of six in every eight rows. The rows with the tassels pulled out are usually the product of a cross of A by B in the previous year. The rows with the tassels left on are the product of C and D the previous year. The seed from the detasseled rows will be sold to commercial corn farmers during the winter and early spring.

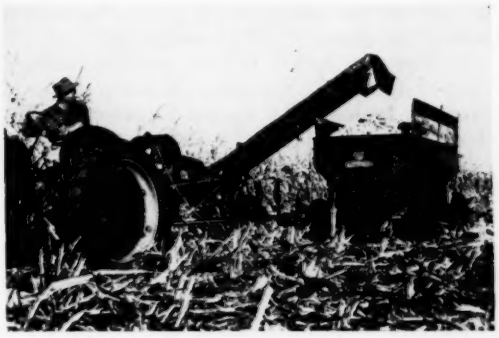


FIG. 25. Tractor pulls a corn-picking machine and a wagon. These machines have reduced the time of corn picking to about one-fifth what it was when hand methods were used. This figure illustrates how it was that stiff stalked hybrids made corn-picking machines really practical. Their use in the past thirty years has increased about fifteen times.

FIG. 23. During July and early August tassels are pulled from about two billion corn plants before the pollen is shed so as to insure cross pollination. Cytoplasmic male steriles, properly used, may eventually do away with a part of this work. In the year 1956 the jobs of the local high school girls are not being seriously threatened.

FIG. 26. On the left a stiff stalked, strong rooted hybrid which stands up stiff and straight under rain and wind conditions which knocked down the old fashioned corn on the right.

per cent of the inbreds which go into the hybrid corn of the central Cornbelt are derived.

In the first decade of the twentieth century Reid corn was on the point of being seriously damaged by men who wanted to overemphasize the Gourdseed side of the Reid corn ancestry. For some years the State Fairs, Farm Journals, and some of the State Colleges tried to set as a standard of perfection a uniform type of rather rough corn with eighteen or twenty rows. Before much damage had been done, hybrid corn came into the picture via Darwin, Beal, Mendel, East, and Shull. Darwin inspired Beal who did the first crossing by the detasseling method for the specific purpose of getting increased yields. East's inspiration undoubtedly goes back to Darwin via Beal. Shull, who probably had a deeper insight into hybrid vigor and a greater faith in its ultimate practicality than East, seems to have derived his inspiration from Mendel. I, myself, in 1910 got my first inspiration for the crossing of inbred strains by reading one of Shull's papers. Later I benefited greatly from contacts with East and his students. East through his students had a tremendous influence on the future of hybrid corn.

When the U. S. Department of Agriculture and the various Cornbelt experiment stations as well as several private individuals began to inbreed and crossbreed corn in a big way in 1921 they naturally turned to Reid Yellow Dent which had been spread far and wide over the Cornbelt by the State Colleges, the Farm Journals, and the Show Corn people. That is how it came to pass that the central Cornbelt corn of today contains at least sixty per cent Reid Yellow Dent blood. Neither East nor Shull worked with Reid Yellow Dent. What they contributed was a scientific method, not superior genetic material. It took men actually living on the land of the Cornbelt states, associating with the corn plants there, to discover just which inbreds out of Reid Yellow Dent and a few other varieties of similar origin would best serve the future.

Looking back we see that the first step forward was when "dent corn" or the "Lorain cross" replaced the eight-row flint corn and thus increased yields by one third. Reid corn was one of the better kinds of dent corn and probably added another ten per cent when it was spread widely over the Cornbelt in the first decade of this century. Finally, during the past twenty-five years hybrid corn, based in considerable measure on inbred strains extracted from Reid corn, has further increased yields fully thirty per cent. Perhaps more important than the increased yields has been the increased strength of stalk and roots which made corn pickers really practical for the first time.

While I personally detasseled every other row of a five-acre field in 1904 and did a little inbreeding work in 1913 I did not get actively into the fight of promoting the revolution in corn breeding until 1919. From that time on I ran many dozens of articles on hybrid corn in the paper of which I was then editor. It takes many people working a long time to break down old

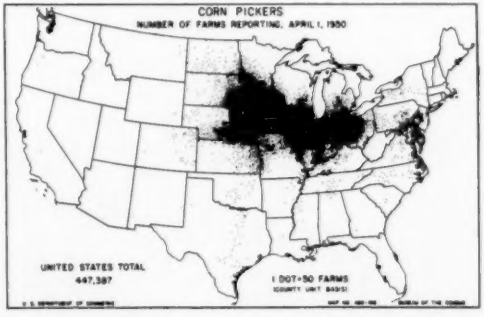


FIG. 27. Where corn-picking machines are found. This map gives the most accurate outline of the true Cornbelt. Kentucky and Tennessee which were the two top corn states in 1839 were no longer in the Cornbelt in 1950. Since 1950 the number of corn-picking machines has increased another 50 per cent. Courtesy of the Bureau of the Census.

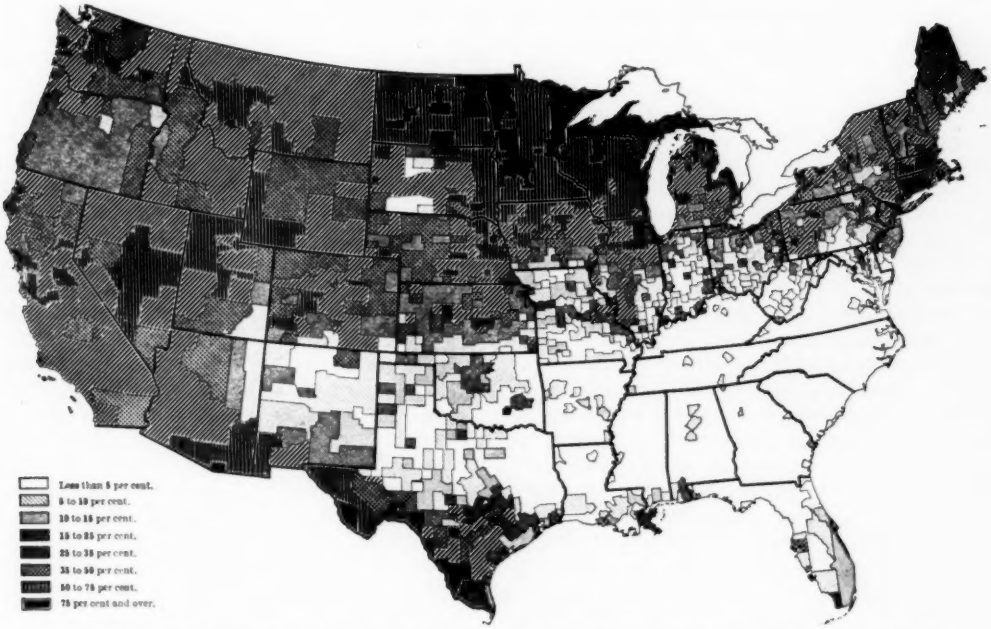

Less than 5 per cent.
5 to 10 per cent.
10 to 15 per cent.
15 to 25 per cent.
25 to 35 per cent.
35 to 50 per cent.
50 to 75 per cent.
75 per cent and over.
Distribution by counties of the foreign-born and natives of foreign parentage in the United States in 1910.

FIG. 28. Distribution of the foreign born and natives of foreign parentage in the United States in 1910. Note that with the exception of a small part of central Indiana the Cornbelt of 1956 is an area where there was a high percentage of immigration from northwestern Europe subsequent to 1830. Courtesy of the Bureau of the Census.

habits. In 1926 I founded the first company devoted exclusively to the production of hybrid seed corn. This company grew very slowly until the great drought of 1934. Then many hybrid seed companies were formed and today ninety-nine per cent of the corn of the Cornbelt is the product of hybrid seed. Because of hybrid corn it is now possible to produce, on eighty-five million acres, more corn than could be produced on one hundred and ten million acres in the old days. The net gain is fully one half billion bushels annually. The end is not yet. The breeders for

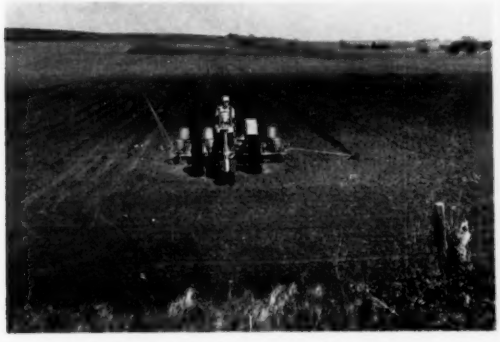


FIG. 29. Planting corn with a tractor.

FIG. 30. Cultivating corn with a tractor.

private companies are spending more than two million dollars annually on research. The U. S. Department of Agriculture and the State Experiment Stations are spending perhaps one million dollars annually. Three or four million dollars to improve a crop worth more than four billion dollars annually is not much when we take into account the very great speed of changes in plant pests, methods of culture, adaptation to new fertilizers, changing climate and the like. No doubt we shall need new corn types when we begin to shell the grain in the field instead of merely picking the ears in the field and passing them over the husking rolls.

In summary let me make it clear that the Corn-belt is a complex—first, of a unique soil and climate; second, of good transportation; third, of well-adapted machinery and fertilizer; fourth, of corn scientifically crossed for specific purposes; fifth, of an ever improving type of livestock to turn the corn into high quality human food; and sixth and most important of all, men and women from Scandinavia, Germany, Ireland, England, Scotland, Holland, and all the rest of western Europe together with the old-fashioned Americans from the eastern seaboard. These men of varied backgrounds utilized the soil, transportation, fertilizer, machinery, and high-powered corn to build, in terms of output per man hour, the most productive agricultural civilization the world has ever seen. An efficient Iowa farmer can, with the help of one man, grow the corn to produce enough meat and livestock products to feed three or four hundred people in town. Abundant, high quality animal protein is the basis of the energetic, vital living which is the outstanding characteristic of the people of the United States. Therefore, we may say that for the foreseeable future the prosperity of the city people of the United States and the Midwestern farmer will rise and fall together. Neither one can long remain prosperous without the other. Both must advance hand in hand into the new territory of new technologies of many kinds. The old frontiers have passed away. The new frontiers will come out of the laboratories of scientific research provided we maintain our social structure by using our present super-abundance constructively.

DISTRIBUTION, ENDEMICITY, AND EVOLUTION PATTERNS AMONG COMPOSITAE OF THE GUAYANA HIGHLAND OF VENEZUELA

BASSETT MAGUIRE

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(*Read November 10, 1955*)

INTRODUCTION

IN THE spring of 1955, we at the New York Botanical Garden had completed the twelfth year of reconnaissance exploration in the Guayana Highland of southern Venezuela and adjacent British Guiana and Brazil, in which sixteen separate expeditions to some twenty-five of the more prominent tabular sandstone mountains of the Highland had been made. This program was prompted by compelling evidence that the sand-

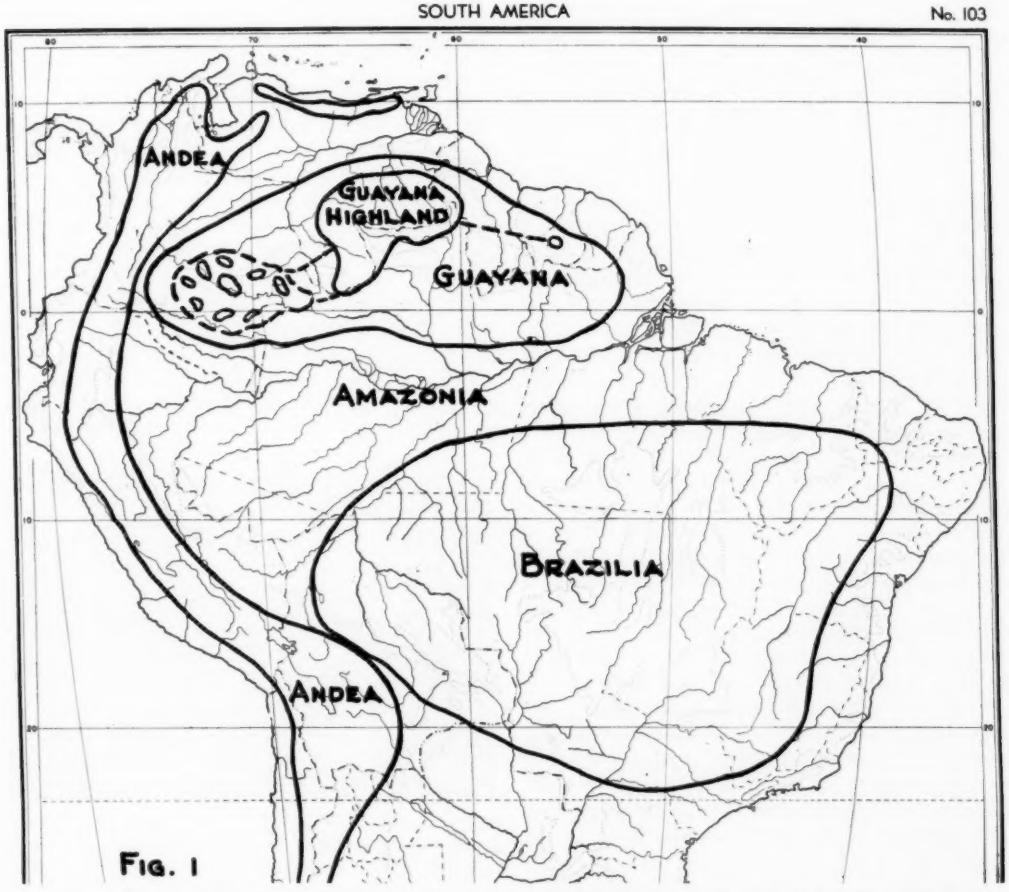

FIG. 1. Map of tropical South America showing general delimitation of the major physiographic provinces of Guayana, Andea, Amazonia, and Brasilia. Area of superposed Roraima sediments outlined within Guayana.

FIG. 2. West-facing escarpment of Mount Roraima, the "Lost World" of Conan Doyle, "discovered" by Robert Schomburgk in 1838, and first scaled by Im Thurn and Perkins in 1884. The original route, shown in the great cleft penetrating the escarpment (in the center of the photograph), remains today the known means of ascent to the summit. (Photograph by Kenneth Jones.)

stone region of Guayana is the seat of a well developed, self-contained, extensive and complex major vegetation. In this distinctive phytogeographic province, endemism had been shown to be extraordinarily high, and relationships of endemic species and genera often obscure.

Historical exploration of Guayana was concerned wholly with the massif of Roraima, which stands at the watershed tricorners of Venezuela, British Guiana, and Brazil. Rising dramatically for more than 5,000 feet above the terraced savannas and wooded plateaus of the Gran Sabana, the great tabular sandstone mountain is ringed by towering vertical red-hued cliffs and buttressed by sharply ascending forested talus slopes. Robert Schomburgk more than a century ago was the first white man of record to see Roraima and to enter upon the sandstones of Guayana.

Succeeding Schomburgk's first visit in 1838 and his second four years later, more than a score of trips were made to Roraima by biologists, geographers, geologists, writers, and adventurers, most notable among the botanists being Appun in 1864, Im Thurn and Perkins who were the first to make ascent to the summit in 1884, twice by McConnell and Quelch in 1894 and 1898, and by Ernst Ule in 1909–1910.

Contemporary botanical exploration of the Guayana Highland began with the further visits to Roraima of Tate in 1927–1928, Pinkus and Perberdy in 1938–1939, and Steyermark in 1944. Of these, the collections made by Tate and Pinkus and Perberdy have been studied and housed at the New York Botanical Garden, as have been the very important collections of Tate made by excursions for the first time into the interior of Guayana to Cerro Duida on the upper Orinoco in 1928–1929, and to Auyán-tepuí in northwestern Gran Sabana in 1937–1938. Steyermark revisited Cerro Duida and made the initial exploration of Ptari-tepuí in the northern part of the Gran Sabana in 1944.

The reactivated program of the New York Botanical Garden, initiated and conducted by Maguire with the assistance of collaborators, particularly Dr. John J. Wurdack (who at this writing is in Venezuela), began with visits to the Kaieteur Plateau and the disjunct Tafelberg in central Suriname in 1944. Explorations continued through the spring of 1955, during which time the chief objectives were: in Brazil: Serra Tepequem and Serra do Sol (Uei-tepuí); in British Guiana: the Imbaimadai Savannas, Mount Ayanganna and Holi-tipu; and in Venezuela on the Gran Sabana: Ilú-tepuí, Ptari-tepuí, and Chimantá-tepuí (two visits were made to Chimantá-tepuí by Dr. Wurdack in collaboration with Dr. Steyermark of the Chicago Natural History Museum), Guaiquinima in the Río Paragua basin; and in Amazonian Guayana: Cerros Sipapo, Guanay, Camani, Yutaje, Parú, Moriche, Yapacana, Huachamacari, Duida, Marahuaca, and more recently to Cerro de la Neblina in southwestern Amazonas

FIG. 3. Cerro Duida on the upper Orinoco River, visited successively by von Humboldt, Robert Schomburgk, and Richard Spruce, but first scaled and explored by G. G. H. Tate of the American Museum of Natural History in 1928. These bold promontories rise to 7,640 feet above the Esmeralda Savannas, which are little more than 300 feet above sea level. (Photograph by Bassett Maguire.)

FIG. 4. Cerro Huachamacari, the Maquiritare "House of the Gods," near Cerro Duida in Amazonian Venezuela. A classic example of the tabular sandstone mountains of Guayana. Ascent was made up the cliffs to the left of "Salto del Dios," which falls for 1,500 feet from the mountain summit. The Culebra savannas in the foreground. (Photograph by Bassett Maguire.)

near the Brazilian and Colombian frontiers, discovered by us in 1953 and visited during 1953–1954.

For a considerable part of the past ten years, while engaged in a field study of *Hevea brasiliensis* (the principal rubber-producing species) and its relatives, Schultes had opportunity to collect in much of the Amazon Basin, where in the Río Negro and its tributaries, the Vaupés and Apaporis, he visited sandstone areas near Araracuara, prominent locality of Martius, and several small sandstone mountains of which Cerros Campana and Chiribiquete are representative.

Material of some 20,000 field numbers, which represent approximately 100,000 specimens, has been collected during the progress of the New York Botanical Garden program. These specimens together with the historical material from Mount Roraima and environs, the Colombian sandstone area collections of Schultes, and the Guayana collections of Tate and Steyermark and of Venezuelan colleagues, Mrs. William H. Phelps Jr., Cardona and Lasser, have provided a body of perhaps 30,000 collections from Guayana. (A more detailed account of the botanical history of Guayana has been presented by Maguire [1] and colleagues.) This material provides the basis upon which our studies must rest.

[1] Maguire, Bassett, Richard S. Cowan, and John J. Wurdack and collaborators, The botany of the Guayana Highland, Introduction, *Mem. N. Y. Bot. Gard.* **8**: 87–96. 1953.

GEOLOGY AND PHYSIOGRAPHY

The Guayana Highland is an ancient mass of great size and diverse physical form. At base lies the Archaean Guayana Shield, the margins of which control the courses of the delimiting Río Orinoco on the north, the Orinoco and the Río Negro on the west, and the Amazon on the south. On the east it is bordered by the Atlantic Coastal Plain.

Superposed over the crystalline Archaean Guayana basal complex are widespread granitic and gabbro intrusives of possible pre-Cambrian age. Upon these were laid down, over extensive areas, enormous thicknesses of sediments—volcanics followed by accumulations of conglomerates and sands, the Roraima Formation. Some interpretation [2] indicates that the Roraima sediments were laid down in Cretaceous Seas (no general marine inundation of Guayana is believed to have occurred since the Cretaceous). Other interpretation indicates that the Roraima sediments are of Triassic or earlier age.[3]

Post-Roraima intrusion of nordic gabbro sills and laccoliths with a maximum thickness of 3,000 feet,[4] and dolorite or gabbro dikes, possibly to be associated with the period of uplift, have probably contributed to the present erosion form of Guayana, and less appreciably to some tectonic deformation and regional dislocation.

Since the period or periods of uplift, from this lens or plateau of sediments there have been weathered out or otherwise formed gigantic lofty isolated mesitas that are characterized by ringing upper vertical escarpments 1,500–3,000 feet high, supported by sharply rising talus slopes from 3,000 to 6,000 feet.

In the Gran Sabana and the British Guiana Pakaraimas, except for the peripheral escarpments and the principal river valleys, erosion has largely not cut through the Roraima sediments. In Amazonian Guayana, at least those areas visited to this time, erosive processes have cut through the sediments deeply into the underlying granitic intrusive or basal complex. Thus, in the Gran Sabana area, the large mesitas of Roraima, Chimantá-tepuí, Auyán-tepuí and others, rise to a maximum elevation of nearly 9,000 feet from base level of the Gran Sabana at 3,000 to 4,000 feet,

[2] Liddle, R. A., *The geology of Venezuela and Trinidad*, Ithaca, 1947.

[3] Stockley, G. M., *The stratigraphy of British Guiana* (Chart), Geol. Surv. Dept. Br. Guiana, 1954.

[4] *Ibid.*; Aguerrevere, S. E. and others, Exploración de la Gran Sabana, *Revista de Fomento* **3**: 644–658, 1939.

whereas in western and southern Amazonas these great tabular mountains, like Duida, Marahuaca, and Neblina, rise to their full majestic height of 7,000 to nearly 9,000 feet above the base level of the tropical rain-forest, at little more than 300 or 400 feet elevation above the sea.

The outlying disjunct Tafelberg of central Suriname indicates that the Roraima deposition extended at least 350 miles eastward of its present periphery. To the west of the Rio Negro, chiefly in the drainage of the Colombian Rios Vaupés and Apaporis, are large areas of terraced sediments and isolated large but relatively low mountains up to 2,000 or 3,000 feet high, consisting of sandstones and conglomerates and exhibiting the typical configuration of the Highland mesitas. It must be assumed that the sediments of these areas are immediately correlatable with the Roraima Formation of the Guayana Highland, and therefore indicate an extension of the original Cretaceous sedimentary deposition 600 miles westward to the margin of the Andean geosyncline. It is suggested, therefore, that the initial Roraima Formation at one time covered essentially (at least) the whole of the Guayana Shield, and that at the present time a small per cent of the original deposit remains.

To the south of the Amazon is the much vaster pre-Cambrian crystalline shield of Brasilia. The Brazilian Shield together with the smaller but comparable Guayana Shield has, since the definition of the continent itself, been the most stable region in South America, and has given form and configuration to the eastern and central part of the continental land mass. Extensive Cretaceous sedimentation [5] seems to represent those of the last submersion of Brasilia.

The geology and history of the Andes are exceedingly complicated.[6] The rocks are composed of Paleozoic and Mesozoic sediments resting on the Archaean complex. Primary elevation took place in the late Cretaceous. Subsequent peneplaning, a second uplift and further peneplaning took place in the Cenozoic. The last elevation, beginning in the Pleiocene and continuing into the Pleistocene (and probably yet in progress), thrust up the peaks of the Cordillera to 20,000 feet and account for the present youthful erosion pattern of the system.

During the Tertiary and possibly as late as mid-Miocene, the Amazon Valley (and probably those of the Orinoco and La Plata) was occupied by shallow seaways, thus accounting for extensive Tertiary deposits in the Amazon Basin. During subsequent elevation it is probable that drainage of the Amazon Basin was westward into the Pacific. Finally, as a result of later elevation of the Andes, the Amazon waters became dammed off, resulting in the formation of enormous inland lakes.[7, 8] When the waters of the inland lakes rose high enough to overflow the eastern rim, the direction of drainage was reversed and the outlet of the huge Amazon Basin became the Atlantic. It is upon the resulting Tertiary-Miocene and Pleiocene sediments and Quaternary alluvial deposits that the youthful vigorous forests of Hylea, the most extensive rain-forests of the world, have developed.

The present topography, land form and indeed the vegetation of the Guayana Highland obviously reflect the character and sequence of historical development, as they have unfolded from the time of deposition and elevation (or successive elevations) of the Roraima sediments. The time sequence of these events in Guayana and the concomitant modification of the vegetation, as they relate to comparable events unfolded in Brasilia, Amazonia and Andea, have profoundly affected the evolutionary development, dispersal and interchange of plants in and among the four major regions.

ENDEMICITY

Of the 25,000 contemporary plant collections from the Guayana Highland, only about thirty per cent have at this writing been studied. Obviously, any conclusion or generalization concerning biological problems to be based upon the entire body of collected material is impossible at this time. And, obviously, the following tentative remarks must be formed from an evaluation of the 7,000 contemporary collections already identified, and from accumulated historical material. Indicated by studies thus far progressed, it may be surmised that the Guayana flora comprises some 5,000 or 6,000 species. It is further indicated that represented in this flora there are possibly as many as fifty endemic genera and possibly between 2,000 and 3,000 endemic species.

[5] Ijzerman, Robert, *Outline of the geology and petrology of Surinam* (Dutch Guiana), 86, Utrecht, 1931.

[6] Darrah, Wm. C., A brief account of the geology of South America, *Chronica Botanica* **7**: 207–211, 1942.

[7] *Ibid.*, 210.

[8] Camp, W. H., Phytophyletic patterns on lands bordering the South Atlantic Basin, *Bull. Amer. Mus. Nat. Hist.* **99**: 211, 1952.

Endemic species are more often not generally distributed over Guayana, but are usually localized on single isolated mountains, on contiguous and related mountain groups, or within regional divisions of the Highland area.

Most of the major plant families of Guayana have developed endemic genera, as is indicated by the following partial tabulation.

Gramineae	*Myriocladus*	19 species
Cyperaceae	*Everardia*	10–12 species
Eriocaulaceae	*Carptotepala*	1 species
Rapateaceae	*Stegolepis*	15–18 species
Bromeliaceae	*Brocchinia*	15 species
	Navia	54 species
Sarraceniaceae	*Heliamphora*	6–8 species
Malpighiaceae	*Sipapoana*	6–8 species
Ochnaceae	*Tyleria*	5–6 species
Ericaceae	*Ledothamnus*	3 species
	Tepuia	3 species
	Notopora	2 species
Rubiaceae	*Chalepophyllum*	4–5 species
	Gleasonia	2 species
	Duidania	1 species

COMPOSITAE

Endemic species are known for all genera of the Compositae occurring in the Guayana Highland except those few of general weedy and widespread nature. Only the genera *Eupatorium* of the chiefly American tribe Eupatorieae, *Calea* of the chiefly American tribe Heliantheae, and members of the largely American tribe Mutisieae will be discussed, since they represent comparatively large groups and seem to compose typical problems relating to the chief topic of discussion, namely, those of distribution, endemicity and evolution.

EUPATORIUM [9]

Eupatorium, with more than 600 species, is almost exclusively American (perhaps a dozen species are extra-American). Most of these, probably 500 or more than eighty per cent, are tropical, of which a relatively small number, twenty-two species, is known at this time to occur in the Guayana Highland. Fourteen or about sixty-four per cent are endemic, six or about twenty-seven per cent are widespread species, and two or about nine per cent are of geographically localized extra-Highland distribution.

[9] Data supplied by John J. Wurdack.

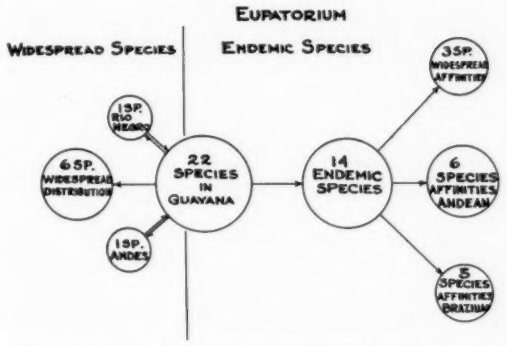

FIG. 5. Chart indicating geographical distribution and putative affinity for Guayanan species of *Eupatorium*.

Of the last pair, *Eupatorium ibaguense* occurs in the Andes of Colombia and Venezuela, and is represented by two distinct endemic varieties in the Gran Sabana region. The other, *E. asperulaceum*, occurs in the Gran Sabana and in savannas of the upper Río Negro basin, which are physiographically similar to the Guayana Highland. These two are to be considered phytogeographically allied with the Guayana species. Of the remaining fourteen endemics, three entities, *E. bathyphlebium*, *E. thurnii*, and *E. karuaiense*, find their nearest relatives among widespread species. Six Highland endemics, *E. pharcidodes*, *E. tyleri*, *E. fuscum*, *E. kavanayense*, *E. tatei*, and *E.* sp. nov., are species with Andean affinities. Five, *E. roupalifolium*, *E. yaviense*, *E. penninervatum* and two undescribed species, find their nearest relatives among southeastern Brazilian species.

There is indicated for the Guayana population of *Eupatorium* a higher degree of relationship with Andean species than with Brazilian. This is perhaps to be expected, since there is a much greater concentration of the genus in the Andes than in Brazil. Except for *E. memorabile* in ed. and *E. penninervatum*, which may represent the beginning of evolution of new lines, the Guayana endemics fit very well into the general phyletic organization of the genus.

CALEA

Calea is a genus of more than 125 species, all tropical American. In Venezuela there are some twenty-five species of which nineteen occur in the Guayana Highland. Only two of these have extra-Highland distribution. *C. deltophylla*, belonging to *Eucalea*, has a limited distribution in the east-

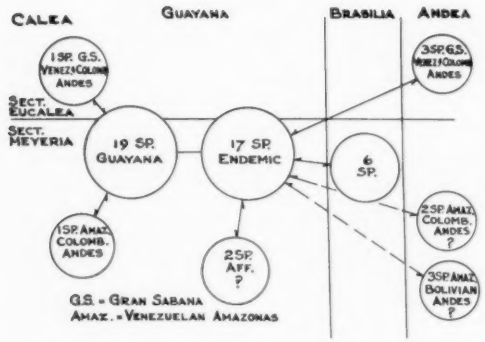

FIG. 6. Chart indicating geographical distribution and putative affinity for Guayanan species of *Calea*.

ern Gran Sabana and the lowland contiguous forest regions of British Guiana and Edo. Bolivar in Venezuela. This species, closely related to *C. berteriana*, a low altitude species of the Orinoco basin and adjacent Colombia, is a recent immigrant to the sandstone Highland. The other, *C. ovalis* of the Sect. *Meyeria*, occurs in the foothills and at low altitude in Amazonian Guayana. It is known otherwise from the nearby llanos of Colombia and the central Colombian Andes. It would appear that this species also is a relative newcomer to the flora of Guayana.

Three species, *C. oliveri*, *C. sipapoana*, and *C. abelioides* of *Eucalea*, a closely interrelated endemic group, find their nearest relative in *C. prunifolia* of the Venezuelan and Colombian Andes.

Of the remaining fourteen endemic species, all belonging to the Sect. *Meyeria*, two, *C. divaricata* of the Gran Sabana and *C. nana* of Amazonian Guayana, suggest no recognizably close relatives. Six species, *C. lucidivenia*, *C. lucida* ined., *C. cardonae*, *C. membranacea*, *C. tricephala*, and *C. punctata*, all closely interrelated, form a close alliance with *C. myrtifolia* and its relatives of southcentral Brazil. *C. linearifolia* ined. is to be allied with *C. longifolia*, also of southcentral and southeastern Brazil.

Calea politii and *C. kunhardtii* suggest superficially an affinity with *C. pennellii* of the Colombian Andes, but this last species belongs to the Sect. *Leontophthalmum*. *C. camani*, *C. esposae*, and *C. phelpsiae* suggest tenuous relationship with *C. robusta* of Bolivia.

All of the four species of the *Eucalea* find their closest relationships with Colombian lowland or Andean species. Five species superficially suggest relationship with elements of the Colombian Andes (two) and of the Bolivian Andes (three). It is probable, however, that superficial resemblance is merely coincidental, and that these species were derived from prototypes not now recognizable. Of the remaining seven species, one obviously finds its nearest relative in Paraná, and the other six, closely interrelated among themselves, find their immediate relatives among a strongly concentrated group of species in southern and eastern Brazil.

MUTISIEAE

The Mutisieae comprises a rather small tribe, chiefly American, with about forty genera and 500 species of the New World tropics (seventeen genera and 100 species of the Old World tropics). The largest genera, *Perezia* with nearly 100 species and *Leuceria* with about seventy-five, are entirely or largely herbaceous. *Mutisia* with perhaps seventy species, *Chuquiragua* with sixty-odd species, and *Nassauvia* with fifty or more species, are shrubby. The plants involved in the following discussion are all woody, some of them medium or even large trees.

In the Guayana Highland there are nine genera of the Mutisieae. Four belong to the subtribe Gochnatinae in which the corollas are regular, and five to the subtribe Gerberinae in which the corollas are bilabiate (or ligulate).

In the group with regular flowers, *Stenopadus*, arborescent with large leaves, prominent many-membered involucres, paleaceous receptacles, and actinomorphic flowers in massive heads, stands as

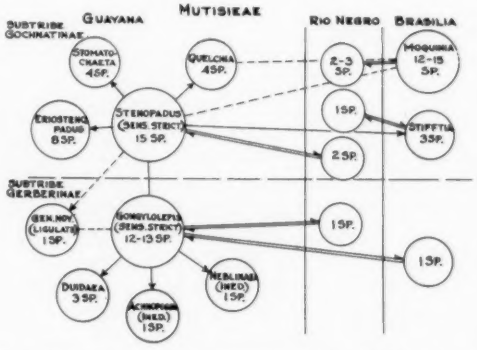

FIG. 7. Chart indicating geographical distribution and putative affinity or derivation of Guayana members of the Composite tribe Mutisieae, and two Brazilian genera *Moquinia* and *Stifftia*.

the central group. Thirteen species, each locally restricted, are confined to the mesita-summits of Guayana. Two species, migrant from the main body, occur in the Río Negro basin, one in a low altitude, white-sand savanna, and the other on a small sandstone mountain in the tributary Vaupés.

Segregate from *Stenopadus* (sens. strict.) are four species of the subgenus *Stomatochaeta* (elsewhere to be treated formally as a distinct genus), all shrubs with small leaves, small few-flowered heads, with receptacular pales restricted to the margins, and the lobes of the corolla stiffly erect.

The subgenus *Eriostenopadus,* with eight species (only one so far described), is likewise a clear-cut segregate of generic stature. In this group, certainly the most specialized, the herbaceous habit is almost attained in the large, soft-stemmed, little-branched, bizarre stature of some of its species. The heads are large, the corollas actinomorphic and pubescent with coiled lobes, the pappus more specialized, and the receptacular pales marginal. One species occurs on Auyántepuí of the Gran Sabana. The remaining seven are known only from the nearby summits of the Chimantá massif.

Quelchia, now with four species, in which the inflorescence is axillary and the head develops but a single flower, was considered by Brown [10] to be allied to the central and south Brazilian genus *Moquinia* (12–15 species). More likely *Moquinia* finds a closer relationship with the basal *Stenopadus.*

FIG. 8. The writer gives scale to a specimen of *Gongylolepis huachamacari,* where it is prominent in the moor-like savanna of the Huachamacari cumbre. The ochnaceous *Leitgebia guianensis* is the dominant heath-like plant in the landscape; less conspicuous is the branched pitcher-plant, *Heliamphora tatei.*

FIG. 9. A close view of the inflorescence of *Gongylolepis huachamacari.* (Photograph by Bassett Maguire.)

Closely related to and derived from *Stenopadus*-proper is the genus *Stifftia* (with three species), which stands morphologically with respect to the prototype much as do *Stomatochaeta, Quelchia,* and *Eriostenopadus.* The center of distribution of the genus *Stifftia* (two species) is in southern Minas Geraës and Goyaz. The third species occurs very locally on sand savannas along the lower Río Negro.

Of the Guayana Mutisiads characterized by bilabiate corollas, *Gongylolepis* with twelve species seems to be the basic genus. Ten species of *Gongylolepis* (sens. strict.) are confined to the Guayana Highland. Two elements, one of them a fruticose reductive species, occur in the Gran Sabana region, the others in Amazonian Guayana. An additional species occurs on white-sand savannas variously along the Río Negro, and another in the eastern Andes of Venezuela and Colombia.

Three derived specialized segregates have been cut off from the large-leaved, arborescent, massive-headed *Gongylolepis. Duidaea,* confined to Cerro Duida, with three species, was recognized by Blake [11] in 1931.

A further morphologically reduced segregate is the monotypic genus discovered on Cerro de la Neblina along the Brazilian frontier in southwesternmost Amazonian Guayana. The single species of this genus, because of its small clustered axillary heads with four or fewer flowers, is a probable bilabiate analogue of *Quelchia* discussed above.

[10] Brown, N. E., Report on two botanical collections made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana, *Trans. Linn. Soc. Lond.* ser. 2, **6**: 42, 1901.

[11] Blake, S. F., in Gleason, Botanical results of the Tyler-Duida expedition, *Bull. Torrey Club* **58**: 496, 1931.

The third segregate of *Gongylolepis* is likewise a monotypic entity, habitally very similar to the suffruticose species of *Gongylolepis,* but its flowers, reduced to four or fewer, are goblet-shaped (instead of trumpet-shaped) and occur in small cymose axillary inflorescences. This entity seems to represent another ultimate reductive line of departure from *Gongylolepis.*

On Cerro de la Neblina, occurring quite commonly on open cumbre savannas and in more or less open *Bonnetia*-bushland, is a shrub with the appearance and habit of *Stenopadus* but with bright red flowers. In the field, after only cursory examination, it was tentatively placed with *Stenopadus.* Upon critical examination in the herbarium, however, it was found that all flowers were completely ligulate, each ligule bearing five essentially equal short lobes. It seems obvious that this plant is a derivative of *Stenopadus,* yet the ligulate flowers would take it across the subtribal line and place it by definition within the Gerberinae.

A superficial search through the genera of the Mutisieae has revealed no genus which could be considered closely related to *Gongylolepis* (and its derivatives), unless it be *Stenopadus* in the Gochnatinae. Both have a remarkable resemblance in habit, leaf-form, and leaf venation.

To recapitulate, in the Guayana Mutisieae, *Stenopadus* and its immediate relatives comprise a compact group of genera of thirty-one species, two of which in *Stenopadus*-proper occur in the Rio Negro drainage system. The nearest relative is the small genus *Stifftia* with its center of distribution in Brasilia on the campos of Minas and Goyaz. With this exception, *Stenopadus* and its cogeners are indigenous to Guayana.

Among the bilabiate members, of which *Gongylolepis* is the center, there are seventeen species of which one, *Gongylolepis columbiana* of the eastern Andes of Colombia and Venezuela, is extra-Guayanan. *Gongylolepis* and its derivatives apparently find their closest relationship with *Stenopadus.* The monotypic ligulate genus of Cerro de la Neblina seems to be an offshoot of *Stenopadus.*

There is little question but that the entire assemblage of Guayanan Mutisieae arose from some prototype of early Guayana history, and have wholly developed therein. It is further indicated that *Stifftia* is in all probability a derivative of *Stenopadus,* as is probably *Moquinia* and possibly other extra-Highland woody genera among the Gochnatinae.

SUMMARY AND GENERALIZATION

The present development and distribution of plants of the Guayana Highland have been brought about chiefly by two sets of interactive conditions: (1) the evolution and dispersal of the indigenous flora as a self-contained population, as (2) it has been influenced and modified by transgression of alien elements from without the periphery of Guayana.

If contemporary interpretation of geological sequence in what is now tropical South America is sufficiently accurately read, its history might have been something like this: The two relatively stable structural land masses of South America, the very extensive Brazilian Shield and the somewhat smaller Guayana Shield, by evidence of sedimentation, were last covered by inland seas during Cretaceous time. Following general elevation, possibly in late or immediately post-Cretaceous times, these two regions have, it is generally believed, not again been subjected to inundation and, therefore, have presented land masses available for continuous habitation by plants until the present time. The vegetation, therefore, of these two ancient areas developed concomitantly, as modified by vicissitudes of changing climate and altering topography of their respective regions. They have enjoyed a continuity not to have been experienced by the vegetation of the intervening Amazon Basin, which, during this period of stability of Brasilia and Guayana, has at least twice (the last time as late as the Pleiocene or even late Pleistocene) been subject to inundation and therefore obliteration.

In Guayana and Brasilia there has independently developed in each area a characteristic and stabilized flora, each showing considerable phyletic affinity with the other. In both, but particularly in Guayana, endemism among this basic flora and derived elements is exceedingly high.

Since the primary elevation of the Andean system in the late Cretaceous, planation and subsequent elevation have at least twice taken place. The last uplift began in the Pleiocene, continued through the Pleistocene, and is probably going on at the present time. The flora of the higher Andes, like that of the Amazon Basin, must, therefore, be a recently derived and developing flora, the latter involving massive migration of temperate floras. However, the Andean montane flora is more largely indigenous and has probably remained peripheral during Andean fluctuation. This flora

shows in many instances considerable phyletic affinity and exchange with that of Guayana.

As presently physiographically defined, the broad, low-altitude, rain forest region of Amazonia (inclusive of the basins of the Río Negro and Orinoco) form an ecologically effective barrier to the migration and interchange of most of the floristic elements of Brasilia and Guayana on the one hand, and to a less extent between Andea and Guayana on the other. Presumably this barrier has been effective since Miocene times, and that massive interchange of phyletic assemblages has not since then taken place. Random exchange of migrants among most phyletic groups has probably taken place primarily by the route of the peripheral Andean montane forests of Amazonia.

As related to the problem of origin, affinities, and geographic migration or derivation, a consideration of certain Composite genera yields some suggestive and provocative evidence.

The large widely distributed genus *Eupatorium* has effected its greatest concentration of species in Andea. Of the twenty-two species of Guayana, six seem to have migrated from or been derived from Andean stock. Five Guayana endemics suggest origin or derivation from Brazilian stock. The remainder show relationship with or are themselves widespread species. One may conclude, then, that the center of distribution and perhaps origin of *Eupatorium* lie in the Andes and certainly not in the Guayana Highland, and that the advent of *Eupatorium* in Guayana is by migration largely from Andea and secondarily from Brasilia.

The genus *Calea* with nineteen species in Guayana seems likewise to provide an instance of centripetal migration in which five species strongly appear to have Andean derivation, and seven of origin in basically Brazilian complexes. Two of the endemic species suggest no recognizable close relatives. Probably *Calea*, in Guayana, is wholly derived by migration from outside, having drawn most strongly on Brazilian elements.

In the Mutisieae there is strong evidence for the indigenous origin and development of the entire Guayana complex.

Of the nine genera now known, all are endemic to Guayana where they probably had their origin. Migration has obviously been centrifugal. Such extra-Guayanan genera as *Stifftia* and *Moquinia* seem to have been derived from *Stenopadus*. The distribution of these two genera and their relatives is entirely Brazilian. There appears to have been no migration of the Mutisieae from Guayana to Andea (except one species of *Gongylolepis*).

MACROMOLECULAR INTERACTION PATTERNS IN BIOLOGICAL SYSTEMS

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(*Read November 10, 1955*)

To THE cell physiologist it has long been apparent that cell function requires the orderly interaction, in space and time, of its myriads of highly complex organelles, each of which is itself a tiny microcosm of ordered arrays of molecules and macromolecules. Structural and chemical organization, at various hierarchical levels of complexity, is one of the most essential properties of living systems. This view is inherent not only in morphological studies of cells and their constituents but also in the investigation of the orderly processes of growth, development, repair, and regeneration. A highly specific structural and functional organization of chemical effectors, called genes, is required by the science of genetics which, though highly developed at the biological level, has only recently started to come to grips with the identification and characterization of these determiners.

Various Greek and Latin names have been devised over the years for the micelles, macromolecules, and giant molecular complexes upon which life processes were thought to depend. For a time it was thought that life resides in such giant molecular complexes and that the cell is merely a large aggregation of such "living" units. Until recent years such ideas were chiefly speculative, forming part of various biologists' systems of thought but seldom coming close to the firing line of laboratory experimentation.

It is perhaps hard for younger students of biology to realize how drastically matters have changed in the last decade or two. Biochemists have fractionated cells and have demonstrated the biochemical role of mitochondria as the "power plants" of the cell; the concept of "energy-rich" molecules, such as adenosine triphosphate (ATP), has become current lingo for the biologist; much has been learned by *in vitro* studies about the ways in which key enzymes and enzyme types, energized by the interplay of "energy-rich" compounds, bring about the biosynthesis of various compounds of biological interest. Other partial systems, such as the microsomes and Golgi material, are also being studied *in vitro*, resulting in slow but steadily growing insight into their biochemical roles. The structural and biochemical study of viruses has enormously increased our understanding of the biomolecular mechanisms of some fundamental life processes.

With the application of modern crystallographic, physical chemical and electron optical analyses to the study of complex substances, such as the proteins, nucleic acids and polysaccharides, has come detailed information about the highly specific structural and chemical organization of these substances. The early highly stimulating concepts of Astbury that these complex substances have an underlying similarity of molecular structure within a given class has been confirmed, in substance if not in detail, by the spectacular work of Pauling and other x-ray crystallographers. The helical chain has, in hardly more than five years, become a familiar concept to the youngest student of biology; the Crick-Watson model of the structure of deoxyribonucleic acid (DNA) has played a leading role in this drama. DNA is recognized as a two-stranded helical chain, collagen is a three-stranded chain; the details of chain structure of other proteins, of RNA and other macromolecules, is rapidly yielding to systematic analysis.

From the knowledge already at hand it has become clear that it is because of the very precise and specific manner in which these macromolecules are constructed that they are capable of interacting with each other and with other species of macromolecules in such a highly specific manner, depending upon the nature of the chemical environment in which the macromolecules find themselves. Even small changes in the precise, specific structure may result in "denaturation" with accompanying biological alterations; mutations may result from lesions in the double helical strands of DNA.

The entire battery of physical chemical methods of isolation and characterization of macromolecules is now being opened up on the biomolecular problem. More and more cases are turning up in

which the material exists in solution as thin (15–25 A), highly elongated (1,000–5,000 A) macromolecules. In most of these cases it is clear that these giant particles are built up by some kind of specific adlineation or "polymerization" of simpler components. It is also clear that from this linear aggregation come new structural and chemical properties not inherent in the simpler components but of great biological importance.

It is the primary purpose of this communication to call attention to some of the remarkable properties of these macromolecules, properties by which they seem to "recognize" each other in solution and, depending upon the chemical nature of the environment, interact with each other—or with other species of macromolecules—to produce highly characteristic structural patterns. This highly precise interaction of macromolecular lattices of tissues is not merely of static, structural significance; it is also highly dynamic. When "energy-rich" substances such as ATP are appropriately combined, enzymatically catalyzed coupling of energy upon the macromolecular lattices may occur. Such phenomena are probably fundamental for most processes of cell physiology.

With increasing complexity of organization come new interaction properties which can be demonstrated to occur but which cannot yet be fully accounted for by physical theory. In the opinion of the author the attack on this problem represents one of the most challenging—and rewarding—lines for future investigations in biophysics and biophysical chemistry. It is possible that theoretical developments of this sort may lead to generalizations concerning the interactions of far more complex systems, including cells and possibly organisms themselves. Obviously such progress must depend upon the slow steady advance in our knowledge of the detailed structure of macromolecules as revealed by crystallographers and chemists. However, it seems likely that only a few characteristic types need be worked out thoroughly in order to gain a working idea of the general plan of molecular architecture of other members of the class.

Meanwhile it is for the biologists to discover and isolate as many macromolecular types as possible and to accumulate evidence concerning their patterns of behavior under varying experimental conditions. It is hoped that studies described in this paper may prove useful as an introduction to the field for the uninitiated and a stimulus to those already engaged in its study.

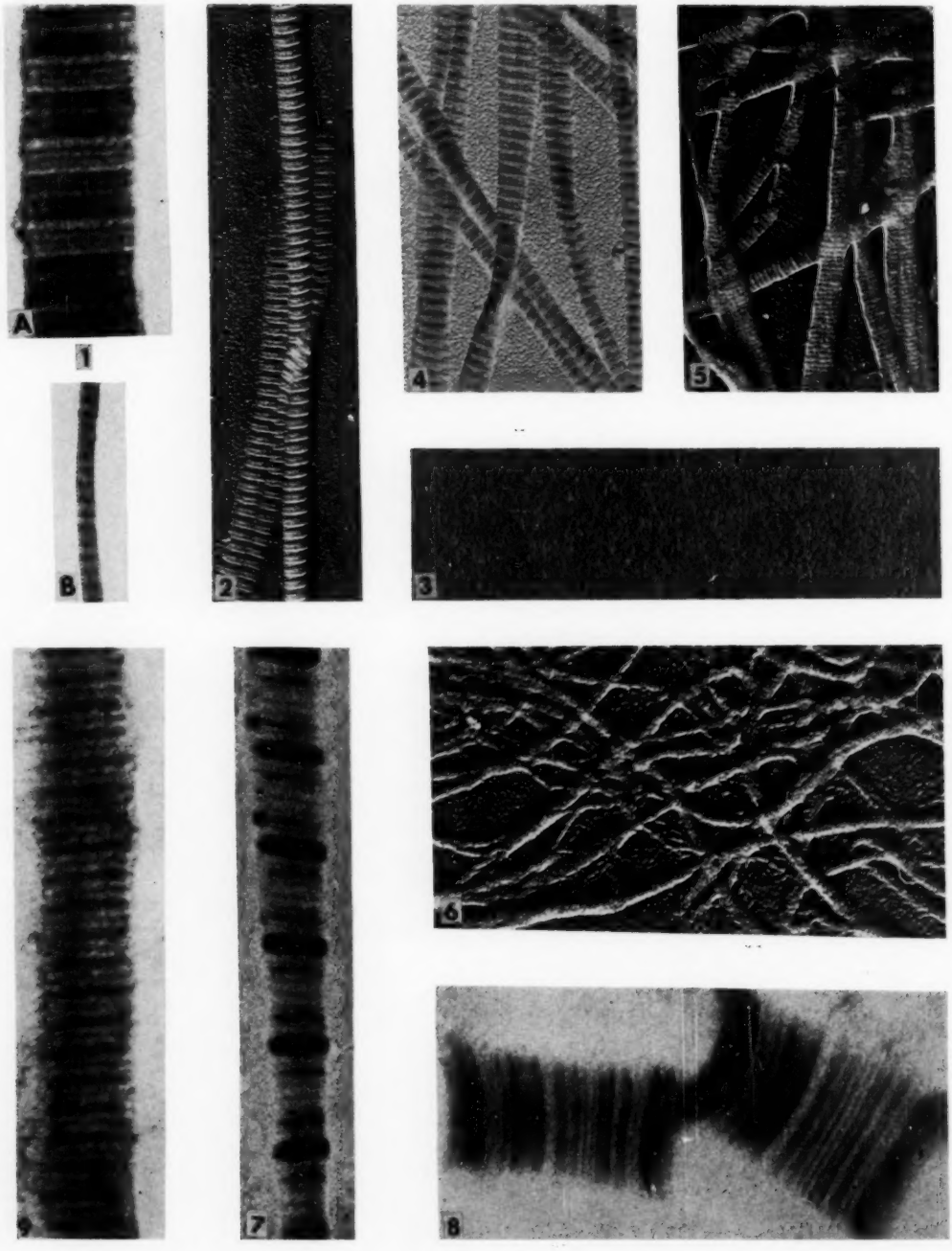
ELECTRON MICROSCOPE EVIDENCE CONCERNING THE ORGANIZATION OF MACROMOLECULAR SYSTEMS

By application of ultrathin sectioning, heavy metal shadowcasting, and so on, it is possible by high resolution electron microscopy of fixed material to discover many new details of the structural organization of cells; to view directly the molecular machinery of the cells. The increasing numbers of the papers now being published on this subject, besides presenting a bewildering, sometimes seemingly contradictory array of observations, reveals the high activity of this field.

Many of the current observations of cell fine structure are of necessity highly descriptive in nature. However, it seems obvious that, already at this early stage in the game, the components of the cell's molecular machinery are essentially fibrous, membranous or granular. It is interesting that these structural modes conform with those considered by an earlier generation of cytologists, chiefly in the last quarter of the nineteenth century, to be the basis of the physical structure of protoplasm. Unfortunately heavy emphasis was laid by individual leaders of cytology upon one of these modes of structure to the neglect of the other modes, thus creating needless word battles and blocks to progress. Each type of structure is of "vital" importance in the chemical economy of protoplasm.

In the present paper we shall consider primarily the fibrous structures because of the light which such studies throw upon the constituent macromolecules and their interaction properties. This is not because the author is insensitive of the importance of the membranous and granular components. Rather it is because the fibrous arrays form certain structural patterns which lend themselves to detailed analysis and thereby to deeper insight into the structure and properties of the component elongated macromolecules.

The structural pattern which has proven so valuable in this analysis is that of a regular cross-striation of fibrils as seen best in the fibrous proteins after staining with heteropolar compounds, such as phosphotungstic acid or osmium tetroxide, or after metal shadowing. The banding consists of an alternation of regularly spaced bands and interbands, representing regions which combine relatively more or less, respectively, with stains or appear thicker or thinner, respectively, in dried material after shadowing. The axial period is very constant in individual fibrils although its



FIGS. 1–9.

value may vary in different fibrils of a population in a given preparation. Detailed intraperiod fine structure may also be observed, constituting molecular "finger prints" of the substances. Small-angle x-ray diffraction evidence was obtained in various laboratories concerning this axial repeating structure. However, only recently has it been possible to interpret the structure in terms of the constituent macromolecules.

The first such banded structure discovered in our laboratory (in 1941) was that of the shaft of the trichocysts of Paramecium after extrusion. Since then many banded structures have been observed, including collagen, fibrin, paramyosin, muscle fibrils, light meromyosin, ciliary rootlets, and others.

Of these, collagen has many advantages for an analysis of macromolecular structure and interaction properties. It will, therefore, form the basis of the analysis upon which the author's point of view will be developed in this paper.

THE COLLAGEN MACROMOLECULE AND ITS INTERACTION PROPERTIES

As shown in figures 1 and 2, the collagen fibril manifests a pattern of regularly repeating bands and interbands with an axial period, usually between 600 and 700 A, and a characteristic intraperiod band pattern. The intraperiod banded fine structure varies considerably from one preparation to another and in different fibrils of the same preparation. As few as two, and as many as a dozen, bands per period may be observed. This variation is due not to differences of resolving power of the electron microscope or of resolution possible in a given preparation but rather to the organization of the collagen macromolecules and their interrelationship with each other axially and laterally, as is demonstrated by the following evidence.

Clues to an understanding of collagen structure came from a study of the acid solutions of collagen and their reprecipitation by salts, early studied by Nageotte, Faure-Fremiet, Wyckoff and Corey, and others. They found that collagen, from rat tail tendon or fish swim bladder, can be dissolved in dilute acetic acid and, by appropriate adjustment of pH and ionic strength, fibrous collagen can again be precipitated. Schmitt, Hall, and Jakus (1942) found that the reconstituted fibrils manifest bands and axial periodicity characteristic of native collagen. In collaboration with Dr. Jerome Gross and Dr. John H. Highberger, the author has made an extensive study of this reconstitution and the light which it throws on the structure of collagen. Details of these studies may be found in two recent papers (Schmitt, Gross and Highberger, 1955*a*, *b*). The main evidence may be summarized very briefly as follows:

The acid solution of collagen contains no formed fibrils, only extremely thin filaments and protofibrils [1] (fig. 3). However from this water-clear, viscous solution may be precipitated at least five differently structured fibrils (and a variety of intermediate forms). By dialysis against solutions of sodium chloride of increasing ionic strength (*ca.* 0.2, 0.4 and 1.0) may be precipitated fibrils having the usual (600–700 A) axial period,

[1] When such extracts are examined with the electron microscope by the improved method very recently developed by Hall (1956) these protofibrils are seen as thin threads about 15 A in width. When the acid solution is "cleaned" of the larger aggregates by the method described by Boedtker and Doty (1954), Hall observed particles about 15 A wide and having lengths in the range of about 1,000 to 3,000 A. He thus observed the tropocollagen macromolecules directly and as individuals rather than as fibrous aggregates.

FIG. 1. Collagen fibril from highly purified steer hide, impregnated with mercury under pressure (courtesy of Dr. Max Swerdlow, National Bureau of Standards) and stained with phosphotungstic acid (PTA). Figure 1A, magnification, 40,000 ×. Figure 1B, magnification, 223,000 ×.

FIG. 2. Collagen fibrils from highly purified steer hide shadowed with chromium. Magnification, 31,000 ×. The kind cooperation of Dr. J. Gross in the preparation of figures 2 to 8 is gratefully acknowledged.

FIG. 3. Filtrate of 0.05 per cent acetic acid solution of ichthyocol (swim bladder collagen). Magnification, 35,000 ×.

FIG. 4. Collagen fibrils (with normal axial period) reconstituted from acetic acid filtrate of ichthyocol by dialysis against 1 per cent NaCl. Magnification, 30,000 ×.

FIG. 5. Collagen fibrils, with one third normal axial period, reconstituted from acetic acid filtrate of ichthyocol by dialysis against 2 per cent NaCl. Magnification, 40,000 ×.

FIG. 6. Collagen fibrils with no axial period precipitated from acetic acid solution of ichthyocol by dialysis against 5 per cent NaCl. Magnification, 35,000 ×.

FIG. 7. Fibrous long-spacing type of fibril precipitated from acetic acid filtrate of ichthyocol by dialysis after addition of purified α-1 acid glycoprotein (0.1 per cent). Magnification, 78,000 ×.

FIG. 8. Segment long-spacing type produced by addition of ATP (0.1 per cent) to acetic acid filtrate of ichthyocol. Magnification, 175,000 ×.

FIG. 9. Bovine fibrin fibril stained with phosphotungstic acid. Magnification, 217,000 ×. Courtesy of Dr. C. E. Hall.

a period of about one-third this value, or tactoidal structures having no banded structure, respectively (see figures 4–6). Addition of certain substances (such as α-1 acid glycoprotein, chondroitin sulfate, hyaluronic acid, or heparin), followed by dialysis, yields a fourth type which we have called "fibrous long-spacing" (fig. 7). The axial period of this form is three to four times that of the "collagen-type fibrils," i.e., chiefly in the range of 2,000–3,000 A. Addition of substances such as adenosine triphosphate to the acid solution produces still another characteristic form which we have called "segment long-spacing" (fig. 8). The segments have the same length distribution as the fibrous long-spacings (2,000–3,000 A) but a very different band pattern. As shown diagrammatically in figure 10, the band patterns in normal collagen and in segment long-spacings are asymmetrical and polarized while that of fibrous long-spacing is symmetrical and unpolarized.

It has been suggested that all of these structural patterns may be explained by assuming that they are produced by aggregation, in different ways, of a common macromolecular type. The macromolecule was called "tropocollagen" because it is capable of "turning into" the normal collagen structure. The existence of these macromolecules was subsequently confirmed by the physical chemical studies of Boedtker and Doty (1955) who concluded that the macromolecules have dimensions of about 14 × 2,900 A.

Tropocollagen macromolecules are themselves polarized in the sense that the distribution of amino acid residues is considered to be constant, characteristic, and polarized. This is symbolized in figure 11 by placing an arrow upon the tropocollagen macromolecules. As indicated in that figure, it is possible to pass reversibly from any structural form to another by appropriate chemical manipulation. The specific types of fibril band structure observed in the electron microscope are considered to be produced by different types of aggregation of the tropocollagen macromolecules with respect to each other. Native-type bands are in "parallel" array, i.e., all pointing in the same direction, but with macromolecular ends staggered by specific fractions of their lengths. When the macromolecules are in parallel array but have ends in register, segment long-spacings are produced. When the ends have no regular relation to each other, tactoidal structures without bands are produced. When the tropocollagen particles are arranged in anti-parallel array, i.e., with arrows pointing in opposite directions, and have ends approximately in register, the fibrous long-spacing structure is produced.

Such an explanation of the origin of the various band patterns implies certain concepts of electron optically observed band structure somewhat as follows: *The macromolecules of tropocollagen are not themselves banded.* Rather they must be visualized as long, triple-stranded protein helices,[2] having side chains extending laterally from the helically coiled strands. If the distribution of amino acid residues in each strand is constant, characteristic, and polarized, then the various types of aggregation of macromolecules will occur by relatively stable bonding of terminal groups of

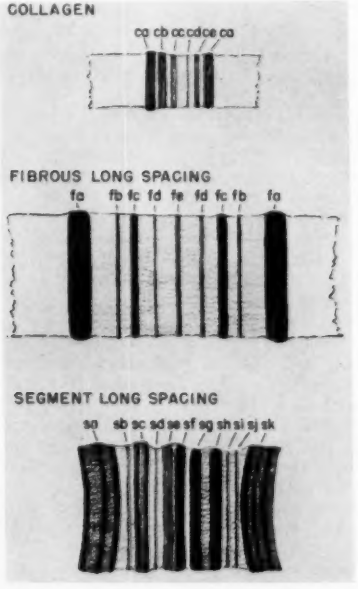


FIG. 10. Schematic representation of the fine structure of collagen, fibrous and segment long spacing. Stained with phosphotungstic acid. Magnification about 200,000.

[2] That the collagen macromolecule is composed of three helically wound strands is strongly indicated by the considerations put forward in several recent papers (Ramachandran and Kartha, 1955; Rich and Crick, 1955; and Cowan, McGavin, and North, 1955). The strands are bonded to each other within the macromolecule by hydrogen bonds. The possibility that this structure permits the macromolecules to assume differing lengths, depending upon the type of "overlapping" of the three partner strands, has been suggested by Highberger and Schmitt (unpublished).

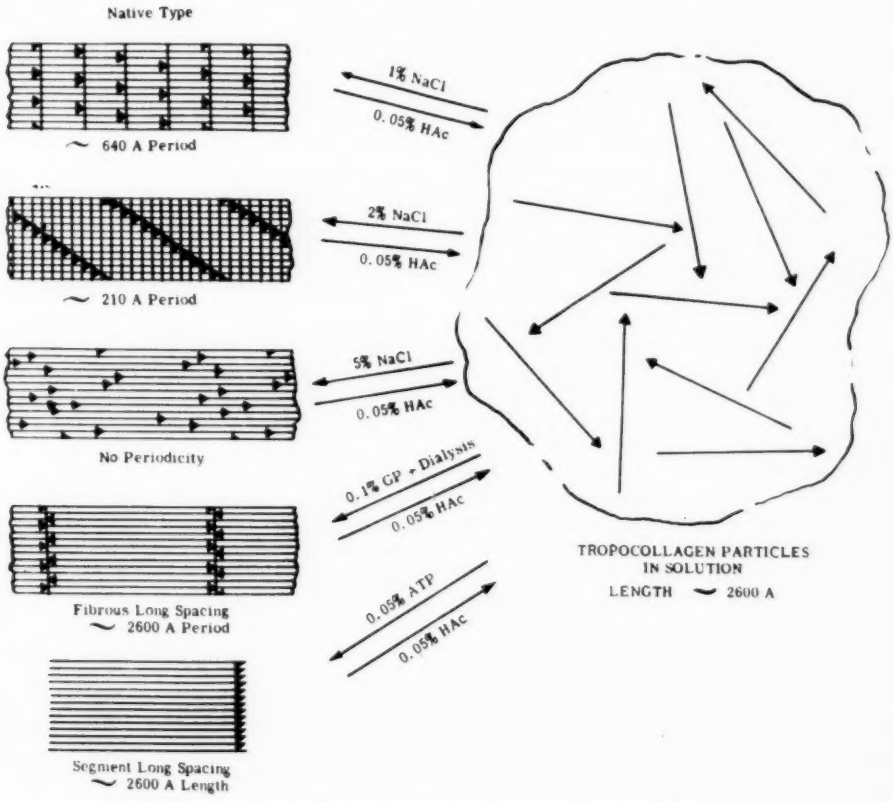


FIG. 11. Modes of aggregation of tropocollagen particles.

side chains of laterally adjacent macromolecules. The particular pattern of side chain interaction will be different with each type of aggregation although all macromolecules and their side chain distributions are assumed to be essentially identical. It is further assumed that band and interband regions, as seen in the electron microscope, are formed when the interacting side chains produce regions of varying degrees of order and disorder. Bear's (1952) suggestion seems reasonable, namely that band and interbands are regions of relative disorder and order, respectively. Bear further assumed that the relative disorder in the band regions is due to the preponderance in these regions of relatively long side chains which have more difficulty in fitting in a well ordered fashion than do the smaller side chains which predominate in the more highly ordered interband regions.

From the above considerations it will be clear that the various patterns of aggregation of protein macromolecules, such as those of tropocollagen, will be determined by: (1) the specific distribution of amino acid residues in the polypeptide chain strands; (2) the specific configuration of the strands, as in one or another type of helix; (3) the type of interaction of axially and laterally adjacent macromolecules, i.e. whether in parallel or antiparallel array, with ends in register, staggered by specific fractions of macromolecular lengths or completely out of register; (4) the concentration of the macromolecules; and (5) the nature of the chemical environment in which the macromolecules find themselves (particularly important are pH, ionic strength and the presence of certain highly charged substances such as acid glycoprotein, nucleic acid, ATP, etc.).

Since the precise helical or other type of chain configuration of most fibrous proteins is known only very imperfectly and the specific linear distribution of amino acids is unknown, it is ob-

viously impossible at the present time to deduce the types of macromolecular arrays which might be possible with a given species of protein under specified conditions. Moreover physical theory is not yet adequate to deal rigorously with the forces likely to be involved in the interaction of such complex macromolecules.[3] Accordingly, for the present, the biologist and biochemist must be content to discover such systems wherever they may be found and, by studying their structural, chemical and interaction properties, to gain information of importance for an understanding of the functioning of the biological system from which the macromolecules were isolated. Such information will also be of great value to biophysicists attempting to deduce general laws governing the interaction characteristics of complex biological systems.

In order to emphasize as strongly as possible, particularly to biologists, the remarkable characteristics of macromolecular systems and their bearing on life processes, we shall mention briefly several other related systems and shall offer a speculation concerning the bearing of these matters on the structure of chromosomes and the nature of the gene.

FIBRINOGEN—FIBRIN

Fibrinogen molecules are thought to have dimensions of about 15 × 600 A. However, when these molecules aggregate, under the influence of thrombin, intermediate polymers are formed having lengths of 3,000–4,000 A (Ferry *et al.*, 1954); these have been observed directly in the electron microscope (Siegel *et al.*, 1953). When these intermediate polymers are activated they form clots composed of fibrin fibrils. As shown by Hawn and Porter (1947) and by Hall (1949), the fibrin fibrils manifest a banded appearance in the electron microscope, the axial period being about 235 A (fig. 9). This period is no obvious function of the lengths of the fibrinogen molecules of which they are composed. According to Ferry *et al.* (1954), fibrinogen molecules may combine with adjacent molecules laterally in a staggered fashion; the intermediate polymer is thus a double row of fibrinogen molecules in staggered array. Although relatively little is known of the details of the structure of fibrinogen and fibrin, some of their features resemble those of the collagen system. Additional interest attaches to this system because it is under the control of a complicated and delicately balanced enzymatic system of kinases and antikinases which determine whether or not the fibrinogen molecules and the intermediate polymers shall react to form the insoluble fibrin fibrils. It is possible that protoplasmic fiber or gel formation characteristically involves some kind of balanced enzymatic control.

[3] A discussion of the nature of these forces was recently held under the chairmanship of Professor Linus Pauling (1955).

PARAMYOSIN, THE CHIEF FIBROUS PROTEIN OF MOLLUSCAN ADDUCTOR MUSCLE

When appropriately stained (Hall, Jakus, and Schmitt, 1945) the fibrils of the adductor muscles of molluscs, such as *Venus mercenaria*, show a band pattern with an axial period of about 145 A and with a geometry of staining regions which is in agreement with Bear's (1944) x-ray findings that the true repeating period is five times this value, or 725 A. This fibrous protein was given the name paramyosin. In an attempt to reconstitute the native structure from paramyosin dissolved in acetic acid, after the manner of the collagen experiments described above, Hodge (1952) obtained a new fibrous long-spacing pattern which he attributed to an antiparallel packing of long macromolecules whose dimensions (*ca.* 15 × 1,500 A) he deduced by physical chemical studies. Also in the author's laboratory, R. Locker (unpublished) succeeded in dissolving the paramyosin macromolecules in 0.6 N KCl (pH = 7.5) and then, by reducing the ionic strength to about 0.15, reconstituted fibrous long-spacing paramyosin similar to that described by Hodge. Although the paramyosin system conforms in main outline with the collagen system, no segment long-spacings of paramyosin have as yet been produced.

The role of paramyosin in producing the long-lasting contraction of the adductor muscles must depend importantly upon the ability of paramyosin macromolecules to interact with each other (and possibly with a myosin-like protein). However little evidence is available as yet concerning this process.

STRIATED VOLUNTARY MUSCLE

It is impossible in this communication to deal adequately with those aspects of the structure of striated muscle and the macromolecular changes which are involved in the processes of shortening or tension production. Any attempt at a defini-

tive discussion would undoubtedly be premature because the basic information available concerning the physical, chemical, and structural properties of the major macromolecular constituents of muscle is still highly provisional and some aspects are still debatable. However, in the present brief section we shall mention only two aspects, one of fact, the other of speculation, but both very pertinent to the present discussion of macromolecular properties.

Hanson and Huxley (1955) adduced evidence favoring the view that the myosin component of striated muscle is located primarily in the A bands. The myosin macromolecules, believed to have dimensions of about 23 × 2,300 A (Weber and Portzehl, 1952), are thought of as lying with axes parallel to the fiber axis between actin filaments.

Isolated myofibrils, when treated with ATP, contract markedly. When such isolated myofibrils are appropriately extracted, the myosin is removed, with the result that the remaining myofibril no longer manifests the typical anisotropic A bands; also the "ghost" myofibril no longer contracts when treated with ATP. However, according to Hanson and Huxley, when such extracted ghost fibrils are bathed in a solution of myosin, the macromolecules of the myosin enter the fibrils in an oriented fashion (though not localized to the original A band region) and the myofibril now contracts after a fashion when ATP is added. It would seem that addition of the myosin macromolecules to the extracted ghost myofibrils reconstitutes fibrils capable of contractility. It was even possible, by exposure of extracted myofibrils of insect flight muscles to a solution containing myosin macromolecules obtained from rabbit psoas muscles, to cause the rabbit myosin to enter the insect ghost myofibrils, reconstituting a "hybrid" fibril which was contractile when treated with ATP. Apparently myosin macromolecules have an affinity for the fibrous component (actin?) of the extracted ghost fibrils which causes them to penetrate the latter in a highly anisotropic fashion.

No consensus exists at the present time regarding the intimate molecular mechanism of contraction. That a reversible combination occurs between two or more fibrous proteins, particularly actin and myosin, seems fairly certain. Although careful electron optical studies have been made by highly competent investigators, it has not yet been possible to visualize directly the macromolecular changes in shortening. Perhaps only when it is possible to identify all of the fibrous structures which can be observed in high resolution electron micrographs of thin sections of muscles, optimally fixed under known conditions of length and tension, in terms of protein entities which have been isolated from muscle and thoroughly characterized structurally and chemically, will it be possible to come to a definitive solution of this difficult problem.

Meanwhile, it may be useful to call attention to a type of macromolecular interaction which may well prove important in biocontractile mechanisms generally. This is the tendency of fibrous macromolecules to coil about themselves to form coiled coils, such as the seven-strand cable discussed by Pauling and Corey (1953). The possibility of strong interaction between two species of fibrous proteins may be due to a built-in complementarity of structure of their macromolecules. If one of the species forms the continuous fibrous lattice of a biological structure, then strong interaction between it and another species of elongated macromolecule, by super-coiling, may cause the entire structure to shorten considerably. Such a mechanism could conceivably account for contractility without change in intramolecular configuration of polypeptide chains. Recent electron microscope studies of thin sections of striated muscle by Spiro (1956) provide some factual basis for such a mechanism.

CHROMOSOMES, GENES, AND MACROMOLECULAR SYSTEMS [4]

The highly specific manner of interaction of protein macromolecules and the great sensitivity of such systems to changes in the chemical environment represent properties which must almost certainly characterize chromosomes to a high degree. Unfortunately, little experimentation with deoxyribonucleic acid (DNA) has as yet been done to demonstrate whether these macromolecules interact with each other, and with protein macromolecules, in the same general manner as do the protein macromolecular systems described above. However, consideration of the properties of the dipteran banded giant chromosomes suggested to the author a possible method of demonstrating that DNA macromolecules possess specific interaction properties to a high degree and this

[4] The substance of this section was subsequently published separately in a brief article under the same title (Schmitt, 1956).

in turn suggested a concept of the fundamental organization of chromosomes and the nature of the gene which will be outlined briefly below.

Definitive knowledge about the types, amounts, and structure of the nucleic acids, proteins, histones, and protamines in chromosomes, particularly such as the banded chromosomes of the insect salivary gland, is still very limited (see Davison, Conway, and Butler, 1954, and Allfrey, Mirsky, and Stern, 1955). However, since the DNA can be extracted by neutral salts under very mild conditions, it must be assumed that the DNA macromolecules thus extracted were held in their specific loci in the banded chromosomes primarily by weak electrostatic bonds. According to Doty (1956) samples of DNA extracted from a wide range of biological sources all have particle weights of about 7×10^6. The contour lengths of the macromolecules are rather long (30,000 A or more) and thin (about 20–25 A). No comparable information exists regarding the protein macromolecules in the chromosomes. However, it may be supposed that the chromosome is composed of a parallel aggregation of an unknown number of species of very long DNA macromolecules (and possibly some RNA macromolecules) together with protein macromolecules, histones and protamines.

In the insect giant salivary gland chromosomes the relative distribution of DNA and protein is indicated by the band pattern (as viewed in ultraviolet or polarized light, with phase contrast or after appropriate staining). The bands and interbands, as viewed in the light microscope, are regions of high and low DNA-to-protein ratios, respectively. Unlike the *periodic* band patterns seen in protein fibrils in the electron microscope, those of the giant chromosomes are *aperiodic;* there is no true repeat over the entire extent of the chromosomes ($\sim 200\ \mu$). The positions of the genes have been localized in the genetic (linkage) maps with respect to these microscopically visible bands, hence with respect to DNA and protein constituents.

What determines the positions of these bands? It is usually supposed that chromosome structure is highly stable over its entire extent and is replicated *in toto,* and that its various gyrations in mitotic and meiotic stages are those of a continuous, if highly coiled, thread. However, the facts of crossing-over, translocations, and inversions, as well as the relative ease of extraction of DNA by salt solutions, indicate that there must be many relatively weak bonds along the length of the chromosomes as well as laterally.

Perhaps some clues may be found in the behavior of protein macromolecules, as previously discussed. In the case of pure collagen (*one* "species" of macromolecule), at least five different band patterns (as well as various intermediate forms), representing as many different types of aggregation of the tropocollagen macromolecules, have been observed. In the case of the banded giant chromosomes let us postulate the existence of a limited number of *species* of DNA and of protein macromolecules, together with histones and protamines. The DNA and protein macromolecules may be expected to aggregate in various ways: individual species of DNA or of protein uniting with each other, with other species of DNA or of protein and DNA macromolecules aggregating with protein molecules. Aggregation may occur in parallel or anti-parallel array, with ends in register, out of register, or staggered according to some pattern of the available reacting groups. Thus, with a limited number of species of DNA and protein macromolecules, it is possible to imagine the formation of aperiodic patterns of bands extending over the entire chromosome ($\sim 200\ \mu$). Certain of the bonds would be stronger than others, thus producing regions relatively stable both to the mechanical forces involved in kinetic and interkinetic phases and to the action of chemical agents.

Another point of great significance should be emphasized. This is that each species of DNA or protein macromolecule occupies a particular position in the linear and lateral array corresponding to the native chromosome—doubtless representing conditions of maximal stability under the environmental conditions prevailing. This suggests that the band pattern of the chromosome, or of parts of it, may be formed *spontaneously* when the constituent macromolecules are available and the chemical environment is favorable. In this case the chromosome need not necessarily be replicated *as a whole.* Rather, when the concentration of the various species of macromolecules is adequate they will spontaneously aggregate after the pattern characteristic of the native chromosome. Such a mechanism requires that the cell be capable of maintaining highly specific chemical environments for the chromosomes at the various stages of cell function because only thus would the various macromolecules spontaneously form the characteristic, stable macro-

molecular pattern required by the genetic and cytological data.

What light does this macromolecular concept throw on the nature of the gene? Most present-day geneticists would agree that the "point determiner" theory of the gene is obsolete. Genes are no longer considered as independent molecules or particles arranged *seriatim* along the chromosome-like beads on a string.[5] Rather it is believed that determiners in one region of the chromosome influence determiners in adjacent and even in remote regions of the same chromosome.

Recent experiments on the transforming factor, bacterial and plant viruses and the phenomena of transduction focus attention on DNA macromolecules as such; highly localized regions, possibly even individual turns of the double helix, are considered to represent individual genes. Such localization, if it does not consider the position of the localized groups in the macromolecules as a whole and the relation of this macromolecule to all the macromolecules in the chromosome, is as vulnerable to criticism as is any point determiner concept.

It is, of course, possible to suppose that the catalytic chemical effector groups involved in gene action occur as highly localized regions of the DNA helical strands. The very stability of such groups as well as their chemical reactivity would still be strongly influenced by the other groups of the DNA macromolecule carrying the groups.

Another possibility is that the chemical groupings which constitute the genes are not macromolecules or even small regions of *individual molecules*. Rather the chemical groupings corresponding to genes may occur in juxtaposition on laterally adjacent macromolecules, either of DNA or of protein. The fit of these helical structures is very precise, thus making possible such a sharing of groups on adjacent macromolecules to constitute a "gene." A nucleoprotein is, in fact, such a complex between a protein macromolecule and a double helical strand of DNA.

The interaction pattern between adjacent macromolecules provides an enormous number of combinations of groups depending upon the orientation (parallel or anti-parallel) and register of the ends of the interacting macromolecules. With the same population of DNA and protein macromolecules it would be possible to obtain, or as the geneticist would say to "activate," a wide variety of genes depending on which species of macromolecules are in contact and on the specific geometry of the packing. Arrays which are stable under certain conditions would be unstable under other conditions.

Gene "activation" would thus be visualized as an appropriate adjustment of the relations between particular macromolecules without essential alteration of the constituent macromolecules themselves. Changes in the chemical environment, such as occur in processes of differentiation and morphogenesis, might well suffice to alter the mutual interrelationship of chromosomal macromolecules. The resulting change might bring into juxtaposition chemical groupings which would constitute different catalytic groups of genes from those which existed in the previous environment. The new catalytic groups might influence chemical reactions which would produce further steps in differentiation and development. Thus would be established the type of feedback mechanism which must almost certainly be involved in the highly regulatory processes of development.

Very recent experiments suggest that the DNA of bacterial viruses (and the RNA of plant viruses), without the protein which is usually associated with it, may suffice to produce infectivity. If it be argued, along such lines, that it is only the DNA macromolecules which contain the genetic activators, it would still be true that, as in the case of the virus mentioned, the protein is required under natural conditions to shield the DNA chemically and mechanically. It could equally well be argued that the protein partner shields certain groups on the DNA and activates others. Thus it is the interaction of adjacent macromolecules, whether of DNA upon themselves or upon protein, which provides the geometric relationship and the capacity for almost infinite modulation, activation, and inactivation of the various groups and which must characterize the chromosomal bearers of the genetic determiners.

[5] The tendency for those who have published papers on the electron optical examination of chromosome structure to pay especial attention to particulate or bead-like structures may reflect the survival of the point-determiner theory in modern guise. From the considerations brought forward in this paper it is unnecessary to suppose that the interactions between adjacent macromolecules, believed to be involved in gene action, need necessarily manifest themselves as bands when viewed with the electron microscope. No such band structure has thus far been reported in DNA or DNA-proteins as examined in the electron microscope.

Fortunately, some of the suggestions here offered are susceptible of experimental proof and efforts are now being made to obtain such proof. In collaboration with Dr. Herman W. Lewis, the author is attempting to dissociate the macromolecular organization of the giant banded chromosomes, by exposure to various salts and hydrogen bond breakers, thus causing the banded structure to disappear. Then, by restoring the altered chromosomes to "normal" environment, it is hoped that it will be possible to reconstitute banded structures [6] (not necessarily with the band patterns of the normal chromosomes). Experiments are also contemplated in which extracts of giant salivary gland chromosomes, demonstrated to be free of particles resolvable with the light microscope, will be treated in a manner calculated to cause the DNA and protein macromolecules to precipitate out (be reconstituted) in a banded, fibrous manner. Success in such experiments would support the macromolecular interaction concept here proposed and possibly suggest ways in which the hypothesis might be tested on intact organisms. Progress in these experiments will be reported in due course.

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[6] The point of view that the macromolecules of chromosomes are bonded together primarily by ionic factors (plus bridges of divalent cations) and may thus be dispersed by treatment with salt solutions of sufficiently high ionic strength has been well stated in an excellent paper on the particulate organization of the chromosome by Mazia (1954). However, the suggestion that dispersed macromolecules of chromosomes may be reconstituted into banded structures, reflecting the specific types of macromolecular interactions and structure suggested in the present paper, have not, so far as the author is aware, been previously suggested.

ELEMENTAL GROWTH RATE OF THE PRIMARY ROOT OF *ZEA MAYS*[1]

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THE apical portion of a growing root has long been recognized as a favorable object for studying cell division and cell differentiation. Mitotic figures may be examined easily in sections and smears of the meristematic portion; various stages of differentiation of several kinds of cells are arranged in linear order from the tip of the root basally, and can be studied largely without the complications presented by the shoot with its nodal organization and leaves. Many microscopical studies of the cellular organization of roots have been made, from the time of Nägeli (1868), Janczewski (1874), and others, to more recent work such as that of Esau (1940) and Williams (1947). It is from such studies of fixed and sectioned material that our concepts of histogenesis and development in the root have largely been derived.

The picture of root structure gained from fixed preparations is essentially a static one. Actually the growing root is a dynamic system in which the cells are undergoing remarkable morphological changes with time. Chemical and physiological changes must certainly parallel the morphological changes. To understand these dynamic processes properly, information gained from the study of fixed sections, or other static studies such as chemical analyses, must be combined with adequate data on growth.

Qualitatively, the nature of root growth has been understood since the classical marking experiments of Sachs (1873) and others. In these experiments, apparently first made nearly two centuries ago by Duhamel (1758), marks are made on a root at known intervals, usually with India ink, and after a period of time the distances between them are measured. These studies have led to the familiar concept of zones of meristematic activity, cell elongation, and maturation. Such experiments are somewhat crude and have usually not been analyzed beyond a recording of the measurements made and a general localization of the region in which elongation is occurring. Nevertheless, they have been repeated by many investigators for various purposes, without any serious attempt to refine them.

Recently some studies have appeared in which growth data obtained by more penetrating methods have been coordinated with data of other sorts from growing roots. The work of Burström (1941, 1949–1951) and of Brown and his collaborators (1949, 1950) may be mentioned. Goodwin and Stepka (1945), working with intact seedlings of *Phleum pratense*, have determined rates of displacement from the apex of recognizable epidermal cells. By plotting these rates against distance from the apex, and differentiating, rates of elongation of portions of the root were obtained which were plotted as a continuous curve against distance from the apex. From these growth data, together with average cell lengths at known distances from the apex, they have derived a curve representing the rate of formation of new transverse cell walls, i.e., of cells. The method of determining growth rates used in the present study is the same in principle as that of Goodwin and Stepka.

In the present paper, methods are described for determining the rates at which marks are displaced from the apex during the growth of roots of intact seedlings of *Zea mays*, and for deriving from these data average rates of elongation with time, which will apply to infinitesimal portions of the root at known distances from the tip. The growth curves so obtained are, it is believed, an accurate quantitative description of the growth in length of the corn root under the experimental conditions used. As such they should have considerable interest in themselves. However, the purpose of this study has been to provide a basis for the analysis of other aspects of the development of the corn root. In forthcoming papers from this laboratory, the growth

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data presented here will be used in conjunction with cell counts, to determine rates of cell formation during growth of the root; with the results of chemical analyses to obtain rates at which chemical constituents of portions of the root, or its cells, are changing during growth; and in the interpretation of the results of metabolic studies.

MATHEMATICAL BACKGROUND AND TERMINOLOGY

From a morphogenetic point of view, it is conventional to regard development of the root as proceeding from the apex of the meristem. This convention is also a useful one in considering the growth of the root. Formulated in analytical terms it amounts to referring the root to a coordinate axis which corresponds to its longitudinal axis of symmetry. It may be termed the X-axis, its origin may be defined as the apex of the meristem, and its positive direction may be defined as toward the basal, mature portion of the root. (Analytically, of course, any point along the root axis might be chosen as the origin, and either direction might be taken as positive.) A point along the root will then be characterized by its distance from the apex, X. It will also be useful to consider an apical segment of the root of length X. During growth, X, the distance of a point from the tip, or the length of an apical segment, will change with time. In symbols,

$$X = f_1(X_0, t) \tag{1}$$

where X_0 is the value of X at $t = 0$.

In any study of growth, interest centers in the *rate* of growth. If the relationship between X and t in the growth of a root were determined experimentally, the instantaneous rate (or velocity) of displacement from the apex of a point at X would be

$$\frac{dX}{dt} \; (= X'), \tag{2}$$

the first derivative of equation (1) at X. This may equally well be considered as the rate of elongation of an apical segment X units long, and is in terms of unit length per unit time. Goodwin and Stepka (1945) have designated it r_x.

Equation (1) might also be differentiated logarithmically to obtain

$$\frac{1}{X} \cdot \frac{dX}{dt} \left(= \frac{X'}{X} = \frac{d \ln X}{dt} \right), \tag{3}$$

the *relative* rate of displacement of a point at X, or the relative rate of elongation of an apical segment X. It has the dimensions, unit length per unit length per unit time. An expression in this form has been termed the "efficiency index" by Blackman (1919) and the "relative growth rate" by Briggs, Kidd, and West (1920; also Fisher, 1920), when applied to data on dry weight of entire plants. Huxley (1932) and other authors have used the term "relative growth" to refer to the allometric relationship, and fo. this reason Richards and Kavanagh (1943) have proposed the term "specific growth rate" for a rate which is referred to size. However, Briggs, Kidd, and West's usage of "relative growth rate" is appropriate, has priority, and has been accepted in studies of plant growth at least.

This expression, $(1/X)(dX/dt)$, does not appear to be a useful formulation of the rate of elongation of the root (see discussion), although relative growth rates are instructive in many growth studies (e.g., Williams, 1946).

It will be useful to consider the rate of elongation, not only of an apical segment X, but also of infinitesimal portions of length of the root, dX. Clearly such a rate will involve, in some form, a second derivative of (1). While X varies with time alone (1), its derivative dX/dt will, in general, vary both with time and with distance from the tip. In symbols

$$\frac{dX}{dt} = X' = f_2(X, t). \tag{4}$$

Differentiation of this expression yields

$$dX' = \frac{\partial X'}{\partial X} dX + \frac{\partial X'}{\partial t} dt. \tag{5}$$

However, if one assumes that the mode of elongation does not change with time (as has been done in the experimental part of this paper), this expression may be simplified. On the assumption that dX/dt changes with X alone, $\partial X'/\partial t = 0$, and $dX'/dX = \partial X'/\partial X$. The notation for partial differentiation may be dropped, and this derivative rewritten

$$\frac{d}{dX}\left(\frac{dX}{dt}\right)\left[= \frac{X''}{X'} = \frac{d}{dt} \ln \left(\frac{dX}{dt}\right)\right]. \tag{6}$$

This may be termed the *relative elemental* rate of elongation, and it will have the dimensions, unit length per unit length per unit time. It may be interpreted as the quotient of acceleration divided by velocity of displacement of a point, i.e., $d(dX/dt)/dt$ divided by dX/dt, but it is not clear what morphological meaning could be given to

such a statement. However, if one considers a small increment of length of the root ΔX, its relative rate of elongation would be $(1/\Delta X)(d\Delta X/dt)$. As ΔX approaches zero, it is replaced by dX, and this expression becomes $d(dX/dt)/dX$. Analytically, dX is an *element* of root length, and its relative rate of change may be termed a relative elemental growth rate.

Of these expressions, (4) and (6) are of most interest. The first, dX/dt, is perhaps the form in which experimental data are most readily obtained. In this form also, growth data can be most conveniently combined with other data on the root, to derive such things as rates of cell formation, or rates of change of biochemical constituents in the root.

For the quantitative description of the pattern of growth in length, the relative elemental rate of elongation (6) appears to be most instructive. Since it is an elemental rate, it applies to each infinitesimal portion, or element, of length of the root, and allows comparisons of the rate of growth of different portions of the root to be made easily. Since it is a relative rate, it has the advantage of referring the rate of growth to the "amount of growing substance," as Blackman (1919) has proposed. Although he and others have argued that such a formulation of growth rates is appropriate *because* of the exponential or autocatalytic characteristics of growth in many organisms, it must be stressed that this is a valid and useful measure, wholly apart from any particular theories of the nature of growth. (The method which shall be used to derive relative rates from experimental data is another question.) This rate also has interesting dimensional properties. As in (3) above, the dimension of length may be cancelled from numerator and denominator, and (on multiplying by 100) one may speak of it as a percentage rate. This property of relative rates has, for example, led Blackman (1919) to stress their value for comparative purposes, and has enabled Kavanagh and Richards (1942) to clarify the dimensional aspects of the allometric relationship.

The analysis of rates of elongation of the root outlined above may be regarded as a special case of Richards and Kavanagh's (1943) general mathematical treatment of growth in three dimensions. In their discussion, points within a growing system are considered to be referred to three rectangular coordinate axes, X, Y and Z. If the positions of points within the system are determined at successive intervals of time during growth, the rate and direction of displacement of each point from the origin of the coordinate system may be expressed in terms of the partial derivatives with respect to time of the three coordinates of the point, $\dot{X}$ (or $\partial X/\partial t$), $\dot{Y}$ and $\dot{Z}$. The rates of displacement for each point are then plotted against the coordinates for its position and a second partial differentiation with respect to the position coordinates is performed. The resulting expression, $\partial\dot{X}/\partial X + \partial\dot{Y}/\partial Y + \partial\dot{Z}/\partial Z$, is the divergence of velocity function of vector analysis. Richards and Kavanagh refer to it as the elemental growth rate in volume per unit volume. In theory at least, it may be determined for any infinitesimal portion of a growing system at an instant of time, and is an analytically precise expression for the rate of growth of that portion, in proportion to the size already attained. They have also derived expressions for the elemental growth rate in length per unit length in two- or three-dimensional systems. Their paper is illustrated with an analysis of Avery's (1933) data on a *Nicotiana* leaf, in which growth is essentially in two dimensions.

In the root, where growth is predominantly by elongation, i.e., one-dimensional, the analysis is simpler, as should be evident from the discussion above. The displacement of a point from the origin is described by the ordinary first derivative, dX/dt, instead of by two or three partial derivatives required when growth in two or three dimensions is considered. The relative elemental rate of elongation (4) is an ordinary second derivative with respect to the one position coordinate. It corresponds not only to Richards and Kavanagh's (1943) elemental growth rate in area or volume per unit area or volume, but also to their rather lengthy expression for rate of growth in length per unit length, which involves the two or three direction cosines, as well as second partial derivatives.

A further comparison between Richards and Kavanagh's (1943) general discussion and that presented here is of interest. In general, the pattern of growth of an organism or an organ may be expected to change with time, as do its size and form. This is certainly true of the *Nicotiana* leaf, which Richards and Kavanagh have considered. An adequate analysis then involves working out the pattern of growth at several points of time, and perhaps a separate presentation of the results at each of these times. Richards and Kavanagh have presented their results in the form of four drawings of the leaf,

in which isopleths and intersecting lines are used to indicate rates of areal and linear growth of portions of the leaf, at four times during growth. If a growing system were to maintain a constant pattern of growth over a considerable time period, a single analysis would suffice for that period of time. This appears to be at least approximately true of the apical growth of the root.

METHODS OF RECORDING GROWTH

Seedlings of the commercial hybrid seed corn, U. S. 13, were used. Grains were soaked in distilled water for 24 hours with aeration, planted on two layers of moist filter paper in Pyrex baking dishes, covered, and allowed to germinate in the dark at 25° C. On the average, roots began to appear about 36 hours after planting. Their growth was followed by photographing a tray containing a number of seedlings at 3-hour intervals with an automatic camera. Measurements of total root lengths were made from the photographs from the time the roots first appeared until they were about 8 cm. long. Elongation is quite exactly linear. The mean rate of elongation of the root as a whole was 1.97 mm.·hr.$^{-1}$ with a standard error of 0.06 mm.·hr.$^{-1}$, as calculated from measurements on 10 seedlings.

For the experiments with marked roots described below, a seedling was selected when its root was 2 to 3 cm. long, and 48 hours after planting. After marking the root by brushing it quickly with a suspension of lamp black in water, the seedling was placed in a rectangular moist chamber constructed of Plexiglas. The root was fitted into a narrow groove, approximately the width of the root, to prevent it from moving laterally as it grew. (Time-lapse motion pictures showed that the tip of an unconfined root performs more or less regular gyrations or circumnutations as it grows.) Roots so confined did not appear to be harmed, and grew at the same overall rate as on filter paper in the baking dishes. In the earlier experiments, the groove was made by stacking strips of blotting paper in such a way as to fill the chamber except for a narrow space in the center. Later, the groove was formed between two parallel bars of Plexiglas, one of which was cemented to the bottom of the chamber; the other was adjustable by two screws extending from the side of the chamber. The groove was lined with moist blotting paper. This later design proved to be better since less manipulation of the root was necessary to place it in position. After placing a marked seedling in the chamber, the groove was adjusted to the proper width, and a Plexiglas cover 0.25 in. thick was sealed with Vaseline to the top of the chamber.

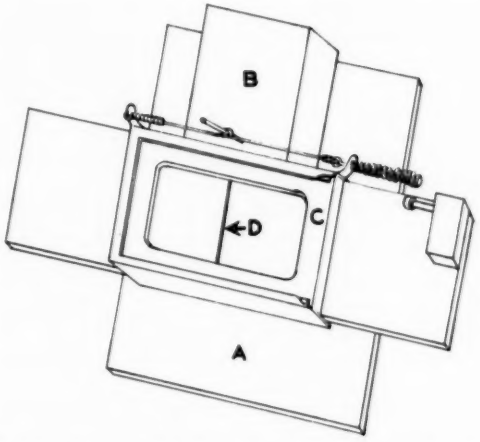

FIG. 1. Diagram of device to record displacement of marks during growth of a root. A. 5 × 7 in. board which fits into back of camera. B. synchronous motor, $\frac{1}{2}$ rev. per hr., with $\frac{5}{16}$ in. shaft. C. carrier for $2\frac{1}{4} \times 3\frac{1}{4}$ in. film holder (not shown). The carrier is moved along the horizontal track by the cord wrapped around the motor shaft. D. slit through which a portion of the root is imaged on the film.

No provision was made to change the gas in the chambers, which ranged in gas volume from 16 ml. to 44 ml. Changes in gas composition during an experiment were estimated from the rate of oxygen uptake of entire seedlings of the size used. It was concluded that these changes were not great enough to necessitate aeration.

The root was photographed during growth with a Bausch and Lomb 5×7 in. photomicrographic camera, fitted with a 101-mm. photographic lens. The camera was tilted so that its optic axis was 30° from the horizontal. A plate to which a microscope mechanical stage was attached was mounted on the base of the camera stand at 60° from the horizontal and perpendicular to the optic axis of the camera. The device shown in figure 1 was fitted into the back of the camera in place of the usual plate holder. It consists of a film carrier which is moved horizontally at constant speed by a synchronous motor. In front of the film carrier is a vertical slit about 5 cm. long and 1 mm. wide, through

which the central portion of the marked root is imaged on the moving film. The principle used in this apparatus was suggested by a method which Kamiya (1950) has used in recording streaming movements in *Physarum polycephalum*.

The camera was set up in a dark constant temperature (25° C.) room. During an experiment, the root was continuously illuminated by a horizontal beam from a small spot light (Spencer Universal microscope lamp), placed about 5 in. from the chamber. A Wratten filter No. 29 (F) was placed before the lamp, so that practically all of the light reaching the root was of wave lengths greater than about 5800 Å.

The chamber containing a seedling was placed in the mechanical stage and lighted with the lamp run at reduced voltage for about 2 hours before the photography was begun. This recovery period was necessary because the overall growth rate of the root was temporarily reduced in marking and mounting it. The light was then turned up, the camera was focussed, and the stage adjusted so that the image of the root filled the lower quarter of the slit. A film holder was placed in the carrier, moved to the left end of the track, and the motor started. During the next 12 hours, approximately, the carrier moved from left to right until it depressed a switch to stop the motor and the light. Contrasty photographic materials were used (Kodak Contrast Process Panchromatic film, Kodak D-11 developer, No. 3 bromide paper).

The authors are indebted to Dr. Lewis N. Lukens for carrying out preliminary experiments by an alternative method. Roots marked with fine India ink lines were photographed at 15-minute intervals, graphs were constructed from the negatives to show the displacement of the marks with time, and analyzed in much the same manner as described below. Although it has several drawbacks, this method has the advantage that individual marks may be recognized.

ANALYSIS OF THE RECORDS AND RESULTS

In the mathematical discussion above, it was suggested that, for an analysis of its growth, the root might be referred to an axis, X, whose origin is at the meristematic apex. Actually the older portion of a root is stationary in relation to its surroundings, and the tip progresses continually during growth. In the photographic records (fig. 2), marks on the older portions of the root

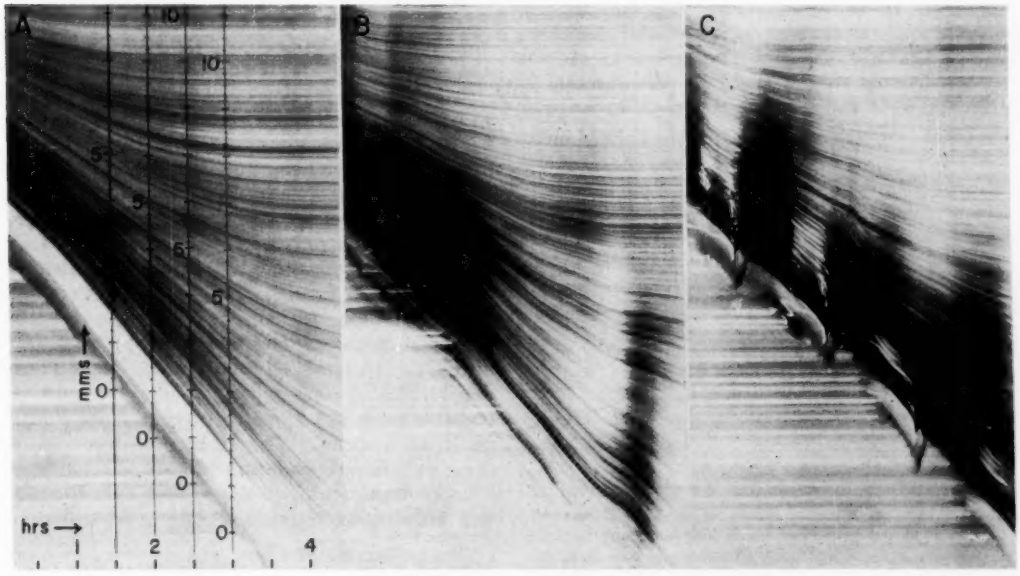

FIG. 2. Representative photographic records of displacement of marks in the growth of three roots. The record shown in A has been marked to illustrate the method of analysis. Vertical lines corresponding to 4 instants of time have been marked off in mm., measured from the tip of the root. In C the record is distorted by circumnutation, and was not used for analysis.

are stationary with respect to the slit at the back of the camera, and register as horizontal lines on the moving negative. After the initial reduction of growth rate involved in mounting the seedling, the tip of the root cap grows downward at a constant rate. It registers on the negative as a straight line, descending from the horizontal (provided that lateral movement of the tip has been prevented). Other marks on the growing portion of the root register as curves, as foreseen by Jost (1907). If these records are referred to two rectangular coordinate axes, the time axis, t, is horizontal. The X-axis, distances along the root, is vertical, but its origin cannot be taken at the apex of the meristem, since that is moving, and furthermore cannot be identified with any certainty.

The following procedure was used. Vertical lines were drawn on the print at selected points along the time axis (fig. 2A). Each of these represents an instant of time, and the intersections of it with curves on the photograph represent the positions of marks along the root at that instant. Using a calibration print of a portion of a mm. rule enlarged to the same scale as the record, distances along the root were marked off on each vertical line at 0.25 mm. intervals, starting at the tip of the root cap. A protractor was used to read the slope of curves which intersected the vertical line at each 0.25 mm. mark. It was so constructed that it could be read directly in trigonometric tangents rather than in angular degrees. Actually, since the readings were made

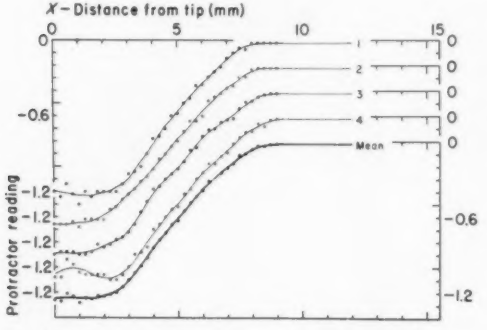

FIG. 3. Data from record shown in fig. 2A. Points represent slopes of curves which intersect each of the 4 vertical lines of figure 2A (numbered 1 to 4 from left to right), at each 0.25 mm. of root length. Means of the 4 slopes are also given. Curves have been obtained from the points by numerical smoothing and have been displaced successively downward to prevent overlap.

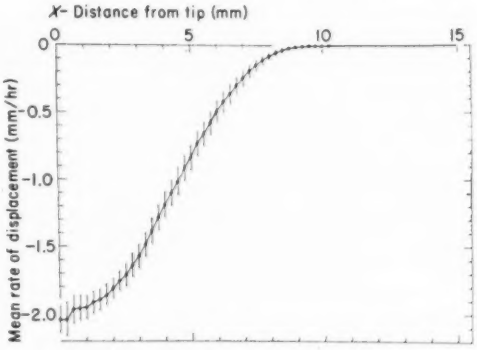

FIG. 4. Mean rates of downward displacement of marks, from 10 photographic records. Vertical line through each point is the 95 per cent confidence interval about each mean.

against the vertical lines drawn on the photographs, the graduations on the protractor represent cotangents of the angles which would appear on a conventional protractor. In rectangular coordinates, the cotangent of the angle which a line makes with the vertical axis is, of course, equal to the tangent of its angle with the horizontal axis.

Representative protractor readings obtained from one of the records (fig. 2A) for 4 instants of time are shown as points in figure 3. Means of the readings are also shown as points.

Mean rates of downward displacement obtained from protractor readings at 4 times on each of 10 records are listed in table 1, column 2. These rates have been calculated by multiplying the mean of the 40 protractor readings for each value of X by 1.667. This factor was derived from calibration prints enlarged to the same scale as the records, on which 1 hour was equivalent to 3.360 cm., and 1 mm. of root length was equivalent to 2.016 cm. on the prints. A slope of -1.00 on the records is therefore equivalent to a rate of displacement of -1.667 mm. per hr. These mean rates are plotted as points in figure 4, together with the 95 per cent confidence limits[2] about each mean. The 10 records from which these data have been obtained were selected from a larger number on two bases: first, that the root was growing at an overall rate comparable to

[2] The confidence limits have been calculated from the total variance about each mean. Analysis shows that the variance between photographs is greater than that within. Values of F range from about 3, within 1 mm. of the tip, to a peak of about 50 at 6 mm. from the tip. The 1 per cent value of F is 3.06.

TABLE 1

RATES OF GROWTH IN LENGTH OF THE PRIMARY ROOT OF *Zea mays* SEEDLINGS, CALCULATED FROM MEANS OF MEASUREMENTS OF 10 PHOTOGRAPHIC RECORDS

X Distance from tip (mm.)	Mean rate of displacement (mm.·hr.$^{-1}$)	95 per cent C.I.	$\frac{dX}{dt}$ (mm.·hr.$^{-1}$)		$\frac{d}{dX}\left(\frac{dX}{dt}\right)$ (mm.·mm.$^{-1}$·hr.$^{-1}$)	
			Mean	Smoothed	Mean	Smoothed
0.00	−2.042	±0.097	0.000	0.000	0.047	0.000
.25	−2.044	±0.119	−0.002	0.001	0.127	0.012
.50	−1.968	±0.102	0.074	0.006	0.132	0.026
.75	−1.957	±0.092	0.085	0.014	0.099	0.041
1.00	−1.952	±0.087	0.090	0.027	0.048	0.066
.25	−1.917	±0.082	0.125	0.047	0.104	0.093
.50	−1.896	±0.078	0.146	0.074	0.131	0.124
.75	−1.857	±0.076	0.185	0.110	0.161	0.148
2.00	−1.815	±0.073	0.227	0.154	0.188	0.181
.25	−1.758	±0.072	0.284	0.202	0.209	0.212
.50	−1.715	±0.082	0.327	0.258	0.232	0.258
.75	−1.642	±0.088	0.400	0.321	0.265	0.291
3.00	−1.576	±0.088	0.466	0.396	0.328	0.323
.25	−1.488	±0.089	0.554	0.483	0.371	0.347
.50	−1.385	±0.095	0.657	0.581	0.409	0.366
.75	−1.286	±0.092	0.756	0.679	0.397	0.379
4.00	−1.189	±0.094	0.853	0.775	0.359	0.384
.25	−1.102	±0.094	0.940	0.865	0.354	0.380
.50	−1.020	±0.096	1.022	0.955	0.348	0.370
.75	−0.920	±0.092	1.122	1.044	0.376	0.361
5.00	−0.838	±0.093	1.204	1.136	0.371	0.352
.25	−0.733	±0.089	1.309	1.224	0.340	0.344
.50	−0.662	±0.087	1.380	1.310	0.331	0.332
.75	−0.581	±0.085	1.461	1.391	0.315	0.317
6.00	−0.496	±0.079	1.546	1.468	0.309	0.299
.25	−0.425	±0.075	1.617	1.540	0.276	0.277
.50	−0.364	±0.069	1.678	1.607	0.242	0.255
.75	−0.300	±0.059	1.742	1.666	0.232	0.235
7.00	−0.249	±0.055	1.793	1.722	0.217	0.212
.25	−0.193	±0 045	1.849	1.772	0.192	0.188
.50	−0.150	±0.038	1.892	1.817	0.168	0.162
.75	−0.112	±0.031	1.930	1.855	0.137	0.139
8.00	−0.081	±0.026	1.961	1.887	0.113	0.114
.25	−0.055	±0.018	1.987	1.912	0.085	0.088
.50	−0.038	±0.015	2.004	1.931	0.066	0.065
.75	−0.024	±0.009	2.018	1.945	0.047	0.045
9.00	−0.012	±0.006	2.030	1.954	0.030	0.030
.25	−0.009	±0.005	2.033	1.959	0.014	0.018
.50	−0.006	±0.004	2.036	1.962	0.004	0.010
.75	−0.005	±0.004	2.037	1.963	0.003	0.004
10.00	−0.005	±0.003	2.037	1.964	0.002	0.001
.25	−0.004	±0.003	2.038	1.964	0.003	0.000
.50	−0.003	±0.003	2.039	1.965	0.002	0.000
.75	−0.003	±0.003	2.039	1.965	0.000	0.000
11.00	−0.003	±0.003	2.039	1.965	0.000	0.000

that of roots grown in the baking dishes, and second, that gyrations of the tip of the root were not unduly great.

It will be seen that all of these rates are negative, and that the mean rate for the tip of the root is −2.04 mm.·hr.$^{-1}$. It is advantageous to consider the tip of the root cap as stationary and to take it as the origin of the X-axis in deriving rates, as well as in designating various portions of the root. This may be done by adding 2.04 to the rate for each value of X. The resulting values represent the first derivatives with respect to time, dX/dt, or rates of displacement of marks from the tip, for each value of X (table 1, col. 4,

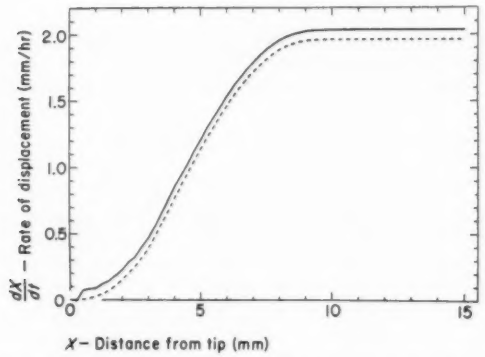

FIG. 5. Rate of displacement of marks from the tip of the corn root. Solid line corresponds to mean rates of figure 4; broken line to the broken line of figure 7.

and fig. 5, solid line). Data for each of the separate records, such as that in figure 3, could also be treated in this way.

Having plotted dX/dt against X, one might evaluate $d(dX/dt)/dX$, formula (4) above, by drawing a smooth curve through the points, and reading slopes of the curve with a protractor, as Goodwin and Stepka (1945) have done. Instead, numerical formulas for the derivative[3] have been applied to columns of dX/dt values, with or without preliminary smoothing.

To give an indication of the nature of the original data, $d(dX/dt)/dX$ values calculated from the single record shown in figures 2A and 3 will first be discussed. The series of measurements for each of the 4 times were first smoothed, using the 9-point smoothing formula (curves in fig. 3); this was also done with the means of the 4 series. The 9-point derivative formula[3] was applied to the smoothed values, to obtain the values plotted in figure 6. As might be expected, these values show greater fluctuations than do the dX/dt values, in spite of the smoothing involved in their derivation. (The propagation of error in this procedure presents a statistical problem which we have not attempted to solve.) The fluctuations appear to be greatest near the tip of the root. Slopes are difficult to read here for at least two reasons. The root cap is covered with a mucilaginous substance which sometimes causes irregular specular reflections of the light (fig. 2C), does not become marked as distinctly as more basal portions of the root, and possibly undergoes swelling or flowing movements not directly concerned with elongation. Secondly, if circumnutations of the root are not completely prevented, they will be most pronounced at the tip (fig. 2C). There are also conspicuous fluctuations in the curves of figure 6 at distances of 2 to 8 mm. from the tip, in the form of secondary maxima and minima. They are reminiscent of the fluctuations which Wagner (1930) found in his graphs of mitotic index against distance from the tip in *Allium* roots. However, the peaks seen in figure 6 are basal to the meristematic region of the corn root. The apparent periodic nature of these fluctuations suggests that they are not wholly due to errors of measurement, but what their significance is cannot be said from the present study. If it is assumed that such secondary maxima and minima of $d(dX/dt)/dX$ progress basally or apically during growth, or occur at different points in different roots, then in random sampling with respect to a number of roots and times of measurement, they should not appear in a curve calculated from the means of a large sample.

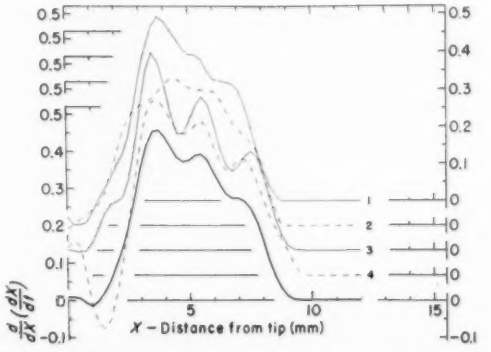

FIG. 6. Slopes of curves shown in figure 3, calculated by a numerical method, and converted to units of mm.·mm.$^{-1}$·hr.$^{-1}$. These are relative elemental rates of elongation of the root represented by figure 2A; calculated from the measurements made at 4 instants of time, and from the means of the 4 series of measurements.

[3] Smoothing formulas are given by Milne (1949). The formulas used in this paper are all based on fitting of third degree polynomials. The 7-point formula, for instance, is $y_3' = (1/21)(-2y_0 + 3y_1 + 6y_2 + 7y_3 + 6y_4 + 3y_5 - 2y_6)$. Formulas for the first derivative have been worked out, using methods such as those which Milne outlines for deriving smoothing formulas. Of these, the 7-point formula is $dy_3/dX = (h/252)(22y_0 - 67y_1 - 58y_2 + 58y_4 + 67y_5 - 22y_6)$, and the 9-point formula is $dy_4/dX = (h/1188)(86y_0 - 142y_1 - 193y_2 - 126y_3 + 126y_5 + 193y_6 + 142y_7 - 86y_8)$, where y_1 is the dX/dt value for a particular value of X, and h is the interval between successive values of X. These formulas are also based on fitting of cubic equations.

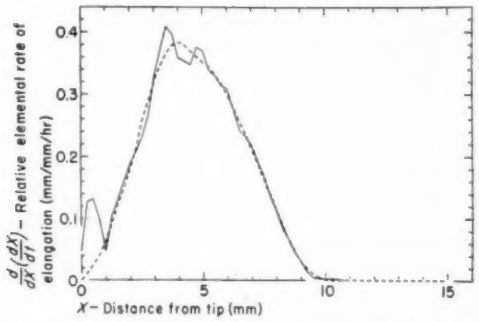

FIG. 7. Relative elemental rate of elongation of the corn root at various distances from the tip. Solid line calculated from the mean slopes of figure 4, with little smoothing. Broken line represents a smoothing of the solid line.

In figure 7 are presented $d(dX/dt)/dX$ values calculated from the mean dX/dt values of table 1, column 2, and figure 4. The solid lines in the figure, and the values in column 6 of table 1, were obtained by applying the 7-point derivative formula[3] directly to the mean rates of displacement. This curve, in other words, represents relative elemental rates of elongation derived from the mean slopes with little smoothing. The authors are skeptical of the reality of the peak in this curve within the first mm. of the tip. Numerically it is due to the fact that the first 2 points are out of line. Slopes are difficult to read here and variability is at a maximum.[2] On the assumption that the rate is 0 at the tip and increases smoothly in the first mm., the values obtained from the 7-point derivation, as described above, for $X = 0$ to 1.0 mm. have been arbitrarily replaced by those shown as a broken line in figure 7 and column 7 of table 1. This assumption is supported qualitatively by experience with the instantaneous photographs of marked roots mentioned on page 491. In this method individual marks can be recognized with more certainty than in the continuous records. Marks placed within a mm. of the tip scarcely changed in position during an 8-hour period, and were not broken into small particles as were marks placed farther back. Careful observation of the tip in the time-lapse motion pictures also suggested that elongation in the first mm. is very slow indeed.

The minimum at $X = 4.0$ to 4.5 mm., with maxima at either side of it, may also be questioned. From the size of the confidence interval about the mean slopes (fig. 4), it seems possible that they may simply be irregularities resulting from inadequate sampling. If this is so, it may be justifiable to smooth them out. This has been done by applying a 13-point cubic smoothing formula to the mean slopes, from 1.25 mm. to 10.0 mm. from the tip, and then applying the 7-point derivative formula to the smoothed values.[3] The resulting values are plotted as a broken line in figure 7 and shown in column 7 of table 1. A single maximum now appears at 4.0 mm. from the tip of the root. A curve showing values of dX/dt corresponding to this smooth $d(dX/dt)/dX$ curve, obtained in part by Simpson's rule for numerical integration, is shown as the broken line in figure 5 and in column 5 of table 1. As will be seen, it corresponds closely with the mean rates of displacement themselves. The principal effect of the smoothing has been within the first mm. from the tip of the root. The limiting value of dX/dt appears to be 1.97 mm. · hr.$^{-1}$ from the smoothed curve, as compared with 2.04 mm. · hr.$^{-1}$ from the unsmoothed data.

In the figures discussed above, rates have been plotted against distance from the tip of the root. It is also instructive to plot them against time. However, the time-axis cannot be taken directly from the photographic records, since the time of recording was considerably shorter than that required for a mark to be displaced from the tip to the older part of the root which is not elongating. In order to find values of time in hours, t, to correspond to various distances from the tip, X, the reciprocals of the mean rates of dis-

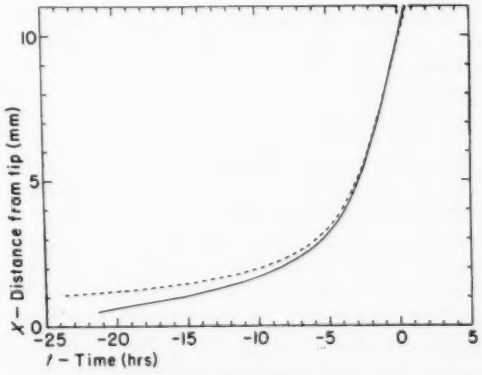

FIG. 8. Displacement with time of a mark from the tip of the root. Time axis has been obtained by numerical integration of the data shown in figure 4. Solid line and broken line correspond to the solid and broken lines respectively of figure 7.

placement, dX/dt (table 1, col. 2), were found. A graph of these values, dt/dX, plotted against X, may be visualized. Values of t for each value of X were then obtained by applying Simpson's one-third rule for numerical integration. Since at $X = 0$, $dt/dX = \infty$, it would have been awkward to have taken $t = 0$ at the tip of the root. Instead the origin of the t-axis was arbitrarily taken to correspond with a point 10.0 mm. from the tip, where elongation has nearly ceased. This procedure was repeated with the smoothed dX/dt values. Figure 8, where X is plotted against t-values derived in this way, may be regarded as a generalization of the photographic records, showing the manner in which a single mark is displaced with time. dX/dt is plotted against t in figure 9. In both figures the solid and broken lines correspond with the solid and broken lines respectively of figures 5 and 7.

DISCUSSION

The expression dX/dt is the rate of displacement of a mark from the tip. It may also be interpreted as the growth rate of an apical segment of the root of length X. Its value at a given point is an integration of the separate growth rates of each small portion of the root between the tip and that point. At 10.25 mm., and greater distances from the tip, it reaches a limiting value of about 2.0 mm.·hr.$^{-1}$ (fig. 5). This rate is equal to the rate of elongation of the root as a whole, which is obtained from measurements of the total length of the root from time to time (see p. 490).

As a quantitative description of the pattern of elongation of the root, the relative elemental growth rate, $d(dX/dt)/dX$, is more useful, since it applies to elements of root length, dX. It is evident from figure 7 that elongation is occurring throughout the apical 10 mm. of the root, but at quite different rates in different portions of this region. A maximum of about 0.4 mm.·mm.$^{-1}$·hr.$^{-1}$ occurs at about 4.0 mm. from the tip. At first sight this rate, 40 per cent per hour, appears astonishingly high (as does Goodwin and Stepka's (1945) maximum rate for the *Phleum* root, 127 per cent per hour), in comparison with other studies of growth in length of plants or plant parts. For instance, Reed and Holland's (1919) much-quoted data on the growth in height of *Helianthus* shoots show a maximum relative growth rate, at an early stage of growth, of about 0.10 cm.·cm.$^{-1}$·day^{-1} (calculated by a numerical method). This amounts to about 0.4 per cent per hour. In flower buds of *Lilium* where growth in length is quite strictly exponential, the relative rate of elongation tends to be constant at about 7.7 per cent per day, or 0.3 per cent per hour (Erickson, 1948). However, such comparisons with relative growth rates of entire plants or organs are not really legitimate. A maximum elemental growth rate refers by definition to that infinitesimal portion of a growing system which is growing most rapidly, and would be expected to exceed the growth rate for the whole system. If for instance the relative rate of elongation were determined for the entire primary root of a corn seedling at various times, a maximum would undoubtedly be found early in its development. Thereafter, since its overall growth rate is constant for several days, the rate would decline hyperbolically as more non-growing tissue is added basally.

Castle (1937: fig. 2) has published data on the growth of the sporangiophore of *Phycomyces*, from which we estimate a maximum relative elemental rate of elongation of about 170 per cent per hour at about 0.8 mm. from the tip.

Figure 8, where X is plotted against t, may be regarded as a generalization of the photographic records. One may determine from this graph the time which would be required for a mark to be displaced from any point along the root to any other more basal point. It will be observed that a day or more is required for a mark to move from a point 0.5 mm. from the tip to a distance of 10.0 mm. from the tip. Since the meristematic apex is about 0.5 mm. from the tip, and elongation has ceased at about 10.0 mm., this may be regarded as an estimate of the time required for a cell to develop from an undifferentiated meristematic initial to a fully elongated cell of the root.

The graph of dX/dt against t (fig. 9) may in a sense be construed as a growth curve for an element of the root.[4] While it is not the purpose

[4] A growth curve is usually considered to be a graph made by plotting some measure or correlate of size as ordinate against time as abscissa. Strictly speaking, this cannot be done for an element of root length, dX, since dX cannot be assigned any finite value. However, since $dX = (dX/dt)\Delta t$, where Δt is an arbitrarily chosen increment of time, the numerical values of dX/dt may be considered as proportional to dX, even though dX/dt does not have the dimensions of length. In other words, the growth curve of an element of root length would have the *form* of figure 9, though no definite values may be assigned to the ordinates.

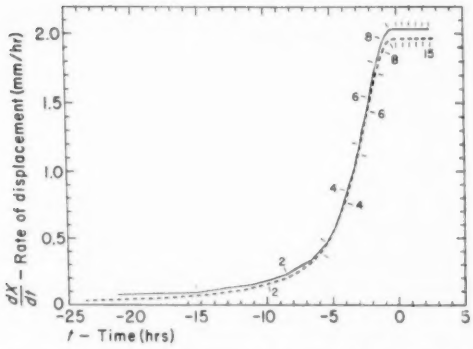

FIG. 9. Rate of displacement of a mark from the tip of the root as a function of time. Solid and broken lines correspond to those of figure 7. Numbers beside the curves indicate distance in mm. from the tip, to which each point corresponds.

of this paper to fit mathematical functions to growth curves, some remarks may be made. This curve (fig. 9) is obviously too asymmetrical to be fitted by the simple autocatalytic equation advocated by Robertson (1923). Furthermore, the first portion of the curve is not exponential in nature, but may be said to have a prolonged lag phase. The sudden inflection and leveling off at a time corresponding to a distance of 10.0 mm. from the tip is similar to the way in which the growth curves of *Lilium* flower buds (Erickson, 1948) quickly level off as the flower opens. These same characteristics of the elongation of elements of the root might also have been shown in derivative form by plotting $d(dX/dt)/dX$ against t.

Finally, it should be emphasized that the relative elemental rate of elongation $d(dX/dt)/dX$ applies to infinitesimal portions of the root, in the sense of differential calculus, and not to the cells of which the root consists. If one is inclined toward the view that a root grows as an organic entity, and that its cellular organization is merely incidental (the "organismal" theory), this should be an adequate description of its growth. If, on the other hand, one holds that the structure and function of a root depend in reality on the structure and function of its cells (the cell theory), it must be realized that the growth of the root as a whole is the resultant of two activities of its cells, cell division and cell elongation. It would be valuable, then, to describe these two aspects of root growth separately. This will be done in the following paper.

SUMMARY

Continuous records of the distance, X, from the tip, of marks placed on growing roots of *Zea mays* seedlings, as these marks are displaced with time, t, have been obtained by a special photographic technique. The curves obtained have been differentiated graphically to obtain *rates* of displacement, dX/dt, of marks from the tip of the root. Numerical differentiation of these rates with respect to X yields *relative elemental rates* of elongation, $d(dX/dt)/dX$, that is, rates of elongation of infinitesimal portions (elements) of the root, relative to their length. This elemental growth rate is small near the tip of the root, rises to a maximum of about 0.40 mm.·mm.$^{-1}$·hr.$^{-1}$ (40 per cent per hr.) at about 4.0 mm. from the tip, and falls to zero at and beyond 10.0 mm. from the tip. The utility of these growth data in the study of other aspects of root growth is suggested.

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RATES OF CELL DIVISION AND CELL ELONGATION IN THE GROWTH OF THE PRIMARY ROOT OF *ZEA MAYS*[1]

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IN THE preceding paper (Erickson and Sax, 1956) a quantitative description of the pattern of elongation of the corn root was presented. Continuous photographic records were obtained of the displacement of marks placed on the root, and from these records the rate of elongation of an apical segment of the root, and the relative elemental rate of elongation at various distances from the tip, were evaluated. It was found that elongation occurs throughout the apical 10 mm. of the root, the maximum relative elemental rate being nearly 0.40 mm.·mm.$^{-1}$·hr.$^{-1}$ at about 4 mm. from the tip.

It is a familiar fact that growth in length of the root involves cell division and cell elongation, and it is the purpose of this paper to extend the analysis so as to describe these two processes separately. Cell numbers and cell lengths have been estimated from macerations and microtome sections of roots. These data have been used together with the growth data of the previous study to calculate the rate of increase in cell number of an apical segment, and the relative elemental rates of increase in cell number, cell length and number of files of cells, at points along the root. A summary of this work has been published (Erickson and Goddard, 1951).

MATHEMATICAL BACKGROUND AND TERMINOLOGY

In deriving rates of elongation (Erickson and Sax, 1956), the root was referred to a longitudinal X-axis, the origin of which was taken at the tip of the root. A value of X then represents the distance of a point from the tip of the root, or the length of an apical segment of the root. In considering the rates at which cells are formed and elongate during root growth, it is useful to define another variable, C, as the total number of cells between the tip of the root and a point X, or the total number of cells making up an apical segment of the root of length, X. In the growth of the root, C will vary both with distance from the tip, X, and with time, t. Analytically

$$C = f_3(X, t) \tag{1}$$

and, in differential form,

$$dC = \frac{\partial C}{\partial X}\,dX + \frac{\partial C}{\partial t}\,dt. \tag{2}$$

If one may assume that the pattern of growth of the root remains constant with time, as regards increase in number of cells, then $\partial C/\partial t = 0$. If this is so, it is apparent that $dC/dt = (\partial C/\partial X) \times (dX/dt)$. Furthermore, if $\partial C/\partial t = 0$, then $dC/dX = \partial C/\partial X$, and it follows that $dC/dt = (dC/dX)(dX/dt)$. This is the same result which would be obtained if C and X were taken as parametric functions of t. In other words, assuming that the cellular growth pattern of the root remains constant with time is equivalent to regarding the length, X, and the number of cells, C, of an apical segment as variables which are related to each other by the parameter time. One may write

$$X = f_1(X_0, t); \quad C = f_4(C_0, t); \quad C = f_5(X). \tag{3}$$

This assumption will be made in the following discussion.

Several methods of expressing the rate of elongation of portions of the root have been discussed (Erickson and Sax, 1956), of which dX/dt, the absolute rate of elongation of an apical segment, and $d(dX/dt)/dX$, the relative rate of elongation of an element of length, dX, appear to be most useful. Rates of increase in cell number, corresponding in form to these, may also be written. The rate of increase in number of cells of an apical segment, C, is

$$\frac{dC}{dt} \; (= C'). \tag{4}$$

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The relative elemental rate of cell formation

$$\frac{d}{dC}\left(\frac{dC}{dt}\right)\left[= \frac{C''}{C'} = \frac{d}{dt}\ln\left(\frac{dC}{dt}\right)\right] \qquad (5)$$

can be derived in a manner similar to that in which the relative elemental rate of elongation was derived, since the assumption of a constant growth pattern implies that dC/dt may be taken as a function of C alone, or of t alone. It is the relative rate of increase of an "element" of cell number, dC. However, C is strictly speaking a discrete variable. If, as is done here, it is treated as a continuous variable, the differential dC at a point must be visualized as a cylinder with a diameter equal to the diameter of the root at that point and an infinitesimal altitude. It does not correspond in any way to a cell, which is the morphological "element" of the root. This discrepancy between the fact of morphology and the mathematical model on which the analysis is based creates no serious difficulty, since the number of cells in the roots studied here is large. Furthermore, these formulas will be applied to data which are averages of determinations on many roots. There is abundant statistical precedent for treating the averages of discrete variables as continuous. One thinks of such data as that on number of children per family in a population, and of the mathematical basis of chemical thermodynamics, where the methods of calculus are used in describing molecular phenomena.

It is also useful to define two other variables in the growth of the root. In older portions of the root, the cells are arranged quite strictly in a number of files. In the meristematic portion of the root, the number of longitudinal files of cells, or the number of cells which would appear in a transverse section, varies at different points. The number of files of cells at a point along the root axis, F_c, is then a function of distance from the tip, X, and hence of time. Since the cells of a root elongate during growth, cell length, L_c, is also a function of distance from the tip, and of time. However, several kinds of cells may be distinguished at a given distance from the tip of the root, and these cells, at least when mature, differ markedly in length. Hence, for the purpose of this analysis, cell length, L_c, must be taken to indicate the mean cell length at a given point along the root axis. Each of these variables may be regarded as a function of time during growth of the root, and it will be assumed that the growth pattern as regards number of files, and mean cell length, also remains constant in time. Although F_c is strictly a discrete variable, and there may be some question about referring the length of a cell to a *point* along the root, no serious error will result from regarding each as a continuous variable with a definite value at each point. The relative rate of increase in number of files of cells at a point is

$$\frac{1}{F_c}\cdot\frac{dF_c}{dt}\left[= \frac{F_c'}{F_c} = \frac{d\ln F_c}{dt}\right] \qquad (6)$$

and the relative rate of change in mean cell length is

$$\frac{1}{L_c}\cdot\frac{dL_c}{dt}\left[= \frac{L_c'}{L_c} = \frac{d\ln L_c}{dt}\right]. \qquad (7)$$

Both F_c and L_c have been defined so as to refer to a point along the root, rather than to an apical segment, as were X and C. They may be said to refer to an element of root length. As a matter of fact, they may be thought of as differentials. In this sense, the relative rates (6) and (7) are elemental rates, though it does not appear necessary to state this explicitly in the definitions.

The relationship between these four variables, X, C, F_c, and L_c, and between the rates derived from them may be deduced. One may first consider a segment of the root made by cutting it transversely at two points, and suppose that its length, the mean length of its cells, and the number of cells appearing in its transverse section were determined. If the segment consists of a series of longitudinal files of cells, each file extending continuously from one end of the segment to the other, the total number of cells of which it consists may be calculated from the formula

$$\text{No. of cells} = \frac{(\text{no. of files})(\text{length of segment})}{\text{mean cell length}}.$$

This formula has been used for estimating cell numbers from studies of sectioned plant material, e.g., by Avery, Piper, and Smith (1945). In the notation used here, the length of the segment may be designated ΔX, and the number of cells which it contains, ΔC. As ΔX approaches zero, this equation becomes $dC = (F_c/L_c)dX$. Dividing by dt

$$\frac{dC}{dt} = \frac{F_c}{L_c}\cdot\frac{dX}{dt}, \quad \text{or} \quad C' = \frac{F_c}{L_c}X'. \qquad (8)$$

Logarithmic differentiation of (8) with respect to time, and rearrangement of the resulting terms

yields

$$\frac{X''}{X'} = \left(\frac{C''}{C'} - \frac{F_c'}{F_c}\right) + \frac{L_c'}{L_c},$$

$$\frac{d}{dX}\left(\frac{dX}{dt}\right) = \left[\frac{d}{dC}\left(\frac{dC}{dt}\right) - \frac{1}{F_c}\cdot\frac{dF_c}{dt}\right] + \frac{1}{L_c}\cdot\frac{dL_c}{dt}. \quad (9)$$

In words, the relative elemental rate of elongation at a point along the root equals the relative elemental rate of increase in cell number, minus the relative rate of change of number of files of cells, plus the relative rate of elongation of the cells at that point. The relative rate F_c'/F_c applies to those cell divisions which lead to an increase in the number of longitudinal files of cells, which may be thought of as those in which the cell plate is formed in a plane parallel to the root axis. Since C''/C' applies to all cell divisions regardless of the plane of separation, the difference $(C''/C' - F_c'/F_c)$ may be regarded as applying to cell divisions in which the equatorial plane is perpendicular to the root axis, that is, divisions which play a part in elongation of the root. Not all divisions are strictly parallel or perpendicular to the root axis, particularly near the meristematic apex, where as Sachs (1878) suggested, the cell files approximate parabolic arcs. Strictly speaking, then, cell divisions with a plane of separation oblique to the axis may be considered to have one component perpendicular to the axis, which enters into the rate F_c'/F_c, and another component parallel to the axis which enters into the rate $(C''/C' - F_c'/F_c)$. A more complete analysis would take account of the planes of division in each portion of the root. However, equation (9) is adequate for the data obtained in this study. It corresponds to the familiar generalization that the growth of a root consists of division and elongation of its cells. The equation, however, is more explicit than such a verbal generalization, and its terms may be evaluated quantitatively.

Each of the terms of (9) is a relative rate. In discussing the relative elemental rate of elongation, $d(dX/dt)/dX$, it was pointed out that the dimension of length may be cancelled from the numerator and denominator (Erickson and Sax, 1956). This is a general property of the relative rate of change with time of any quantity. By virtue of this property, the terms of (9) are additive, even though the variables to which each refers differ in their dimensions.

In the experimental part of this study, each of the time derivatives discussed above has been evaluated. While the relationship between the distance, X, of a point from the tip and time has been determined directly (Erickson and Sax, 1956), it appears to us to be experimentally impossible to relate the other three variables, C, F_c, and L_c, to time directly. Their relationship with X may, however, be determined, and since X is known as a function of time their time derivatives may be calculated. For instance, if the number of cells in an apical segment, C, is determined as a function of the length of the segment, X, the derivative, dC/dX, number of cells per unit length, may be determined. Then dC/dt, the rate of cell formation by an apical segment, is the product of dC/dX and dX/dt, at each distance from the tip. The relative elemental rate of cell formation (5) may be obtained by taking dC/dt as a function of X and finding the derivative $d(dC/dt)/dX$ at the desired points. These values divided by corresponding values of dC/dX give values of $d(dC/dt)/dC$. Similar derivatives of other variables, e.g., formulas (6) and (7), may be evaluated similarly. There are other possible methods of evaluating these rates from the primary data, but this method is well suited to the devices of numerical analysis.

EXPERIMENTAL METHODS AND RESULTS

As in the previous study (Erickson and Sax, 1956), seedlings of the commercial hybrid seed corn, U. S. 13, were grown in the dark at 25° C. Seedlings with roots from 2 to 3 cm. long, and as straight as possible, were selected for determinations of cell number, cell length, number of files of cells, and for counts of the number of cells in various stages of mitosis. For all of the determinations, roots were cut into segments by means of Gillette Thin razor blades (0.004 in. thick), in small jigs, made up of alternate vanes of sheet aluminum and 0.004 in. shims, bolted or riveted together (fig. 1). Three jigs have been used to cut successive segments approximately

FIG. 1. Jig used in cutting roots into 1-mm. segments.

TABLE 1

CALIBRATION OF JIGS USED IN CUTTING SEGMENTS OF ROOTS

X—Distance from tip of root (mm.)		ΔX—Length of segment (mm.)	0.95 Confidence interval
Nominal	Actual		
0.5-mm. jig:			
0.0	0.000		
0.5	0.443	0.443	±0.021
1.0	0.970	0.527	±0.030
1.5	1.497	0.527	±0.009
2.0	2.021	0.524	±0.006
2.5	2.542	0.521	±0.011
3.0	3.066	0.524	±0.013
3.5	3.573	0.507	±0.010
4.0	4.113	0.540	±0.009
4.5	4.619	0.506	±0.017
5.0	5.142	0.523	±0.010
1-mm. jig:			
0	0.000		
1	0.954	0.954	±0.014
2	1.854	0.900	±0.016
3	2.734	0.880	±0.012
4	3.628	0.894	±0.012
5	4.509	0.881	±0.009
3-mm. jig:			
0	0.000		
3	2.966	2.966	±0.025
6	6.060	3.094	±0.031
9	9.100	3.040	±0.018
12	12.151	3.051	±0.043
15	15.281	3.130	±0.037

0.5 mm., 1 mm. and 3 mm. long, respectively. A number of roots were placed in a jig, blades were placed loosely in the slots, and all the blades were pushed down at once. The blades were then removed one at a time and the segments sorted out. Each jig was calibrated by placing razor blades in the slots and pushing them down onto a piece of paraffin-coated card. The distances between marks made by the edges of the blades were then measured microscopically. These calibrations are listed in table 1.

CELL NUMBER

Two series of cell counts have been made, on 0.5-mm. and on 3-mm. segments. The segments were fixed in Navashin's fixative in 1-ml. test tubes for 48 hours, washed in water, hydrolyzed in N HCl for 1 hour at 60° C. and digested with pectinase at 35° C. for about 5 days. The pectinase solution contained 50 mg. of the dry preparation (Nutritional Biochemicals, Inc.) per ml. of a citrate-phosphate buffer at pH 4. After digestion, most of the pectinase solution was carefully removed and the segments were broken up by stirring at about 1,000 rpm. with a small stainless steel stirrer. The resulting cell suspension was then transferred by repeated washing to a 6.5-ml. hematocrit or a 15-ml. centrifuge tube, and diluted to volume. While stirring with a stream of air from a fine capillary tube, samples were withdrawn from the suspension and placed in a hemocytometer slide, with a chamber depth of 0.2 mm.

For the series of counts on 0.5-mm. segments, 4 groups of 10 roots each were cut so as to yield 10 successive segments from each root. For the second series of counts, 4 groups of 6 roots each were cut into 5 successive 3-mm. segments. The first series thus yielded 40 cell suspensions, and the second, 20 suspensions. Ten hemocytometer fields, each 4.0 mm. square, were counted for each suspension, making a total of 40 counts for each segment. From these counts, the total number of cells in each segment was calculated, and the 0.95 confidence interval about each of the totals was determined from the variance of the separate counts. The results of both series of counts are given in table 2, and are plotted as histograms in figure 2.

TABLE 2

CELL COUNTS ON SEGMENTS OF ROOTS

X—Distance from tip of root (mm.)	ΔC—Number of cells per segment	0.95 Confidence interval	$\Delta C/\Delta X$—Mean number of cells per mm.
0.5-mm. segments:			
0.000–0.443	2,890	± 670	6,520
0.443–0.970	28,200	±3,990	53,520
0.970–1.497	44,500	±6,140	84,440
1.497–2.021	47,510	±4,340	90,680
2.021–2.542	33,060	±4,340	63,450
2.542–3.066	20,770	±2,080	39,640
3.066–3.573	15,250	±1,620	30,070
3.573–4.113	11,210	±1,130	20,760
4.113–4.619	8,140	± 880	16,090
4.619–5.142	8,400	±1,060	16,060
3-mm. segments:			
0.000– 2.966	173,260	±10,530	58,420
2.966– 6.060	56,050	± 3,490	18,120
6.060– 9.100	31,320	± 2,200	10,300
9.100–12.151	31,260	± 2,260	10,240
12.151–15.281	30,180	± 1,930	9,640

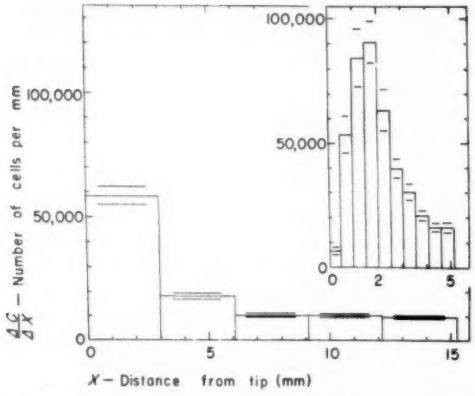

FIG. 2. Mean number of cells in successive segments of the root. Base of each bar is proportional to length of segment, area of each bar, to mean cell number.

NUMBER OF FILES OF CELLS

A number of roots were cut into 5 successive segments with the 1-mm. jig, fixed in Navashin's fixative, imbedded in paraffin, sectioned and stained, for counts of the number of cells which appeared in transverse section, F_c. Care was taken to obtain a complete ribbon from each segment, and to mount the sections in order. Since the length and location along the root of each segment was known from the calibration of the jig, it was possible, by counting, to determine the distance from the tip of any transverse section. Selected sections were photographed and printed at a large scale. All the cells in each print were counted. The 51 separate counts are plotted as points in figure 3, together with a line fitted to the points as described below.

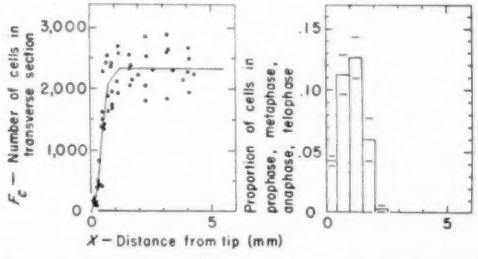

FIG. 3. Number of files of cells at various distances from tip of root. Dots are separate counts on transverse sections. Line was fitted to points by a numerical method.

FIG. 4. Mitotic indices of successive segments of the root.

CELL LENGTH

Another group of 1-mm. segments was fixed, imbedded, and sectioned longitudinally, for measurements of cell length. The most nearly median section of each segment was photographed and printed at a large scale. Since the original lengths of the segments were known from the jig calibrations, the location and length of each cell could be estimated quite accurately, without taking into account shrinkage during fixation and dehydration, nor the magnification at which the prints were made. The photograph of each segment was subdivided into 10 transverse strips, and cells were chosen for measurement by making 10 ink spots in each strip, more or less at random. It would have been desirable to have taken the cells at random from a transverse segment of the root, rather than along a diameter, but this has not seemed feasible. Measurements were made on 5 photographs for each 1-mm. segment, making a total of 50 cells measured for each 0.1-mm. strip. Means of each 10 measurements are plotted as points in figure 5, together with a solid line which passes through the mean of the 50 cell lengths at each distance from the tip.

This direct method of estimating cell lengths has not been continued beyond 4.5 mm. from the tip because of the great variability in length, which necessitates large numbers of measurements, and of the difficulty in obtaining complete sections of the longer cells of the stele, in the mature portion of the root. Mean cell lengths may be estimated from other data, as described below, and these indirect estimates, shown as the

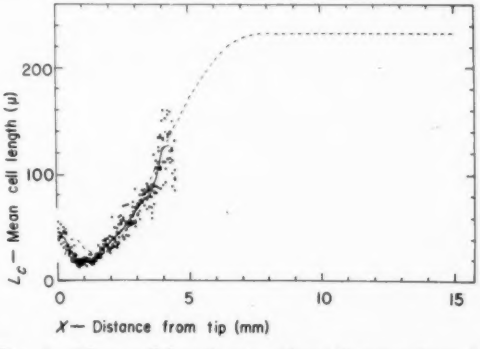

FIG. 5. Mean cell lengths at various distances from tip of root. Dots are means of 10 measurements each. Solid line passes through mean of 50 measurements at each distance. Broken line calculated from other data.

dashed line in figure 5, are in satisfactory agreement with the direct measurements.

MITOTIC INDEX

As a check on the indirect methods for deriving rates of cell division described below, 0.5-mm. segments have been macerated for counts of the number of cells in each stage of mitosis. The segments were fixed in a mixture of 2 parts of absolute ethanol and 1 part of glacial acetic acid, and changed to 70 per cent ethanol for storage. They were macerated (Warmke, 1935) by treatment for 2 min. with a mixture of equal parts of 95 per cent ethanol and concentrated HCl, returned to the acetic acid-ethanol mixture for 5 min. and stained in a 1 per cent solution of orcein in 45 per cent acetic acid for another 5 min. The segments were kept in 1-ml. test tubes during these changes. They were then broken up by tapping with an unground ball-tipped glass pestle, which fitted loosely into the test tube. The segments were to a large extent broken up into individual cells and small clumps of cells which remained in suspension for some time. A drop of the suspension was mounted, and each cell encountered in traversing the slide with a mechanical stage was scored for its stage of mitosis. Five samples of 10 roots each were cut into segments, macerated and scored. Two slides were made from each maceration and 500 cells scored on each slide, making a total of 5,000 cells examined for each 0.5-mm. segment. In table 3 the numbers of cells judged to be in interphase (I), prophase (P), metaphase (M), anaphase (A) and telophase (T) for each segment are given. Mitotic indices have been calculated from these data by dividing the number of cells in prophase, metaphase, anaphase, and telophase by the total number of cells scored (PMAT/IPMAT). In figure 4 the mitotic index and 0.95 confidence interval are plotted for each segment. It is apparent that the mitotic index is at a maximum between 1.5 and 2.0 mm. from the tip of the root cap, and that mitoses do not occur beyond about 2.5 mm. from the tip.

METHODS OF CALCULATION

It has been demonstrated in the mathematical section that rates of change with time of cell number, number of files of cells, and cell length can be estimated by using the determinations of these quantities together with the growth measurements. These rates have been estimated by extensions of the numerical methods of analysis (Milne, 1949) which were used in dealing with the data on elongation of the root.

NUMBER OF CELLS PER UNIT LENGTH

In the mathematical discussion above, C, the number of cells from the tip to any point along the root, was regarded as a function of X, the distance of that point from the tip. One might construct a graph of C against X from the data of table 2, by cumulating the cell counts for the separate segments to obtain successive values of C, and plotting these against the values of X at which the roots were cut. If this curve were suitably fitted and differentiated, values of dC/dX for various values of X would be obtained. Since dX/dt was evaluated at 0.25-mm. intervals along the root, and the cell counts apply to 0.5-mm. and 3-mm. intervals, interpolation of dC/dX to each 0.25 mm. of root length would be desirable.

It has seemed preferable to evaluate dC/dX by fitting a smooth curve to the histograms of figure 2. In plotting the data in histogram form, the base of each bar has been made proportional to ΔX, the length of the segment, and its altitude

TABLE 3

MITOTIC COUNTS ON 0.5-MM. SEGMENTS OF ROOTS

X—Distance from tip of root (mm.)	Number of cells scored	Number of cells judged to be in					Mitotic index	0.95 Confidence interval
		I	P	M	A	T		
0.000–0.443	4,439	4,251	124	19	26	19	0.0424	±0.0039
0.443–0.970	5,000	4,437	357	54	66	86	0.1126	±0.0160
0.970–1.497	5,000	4,368	364	60	97	111	0.1264	±0.0169
1.497–2.021	5,000	4,701	173	32	48	46	0.0598	±0.0172
2.021–2.542	5,000	4,985	5	3	5	2	0.0030	±0.0025
2.542–3.066	3,000	—	0	0	0	0	0.0000	—
3.066–3.573	2,000	—	0	0	0	0	0.0000	—

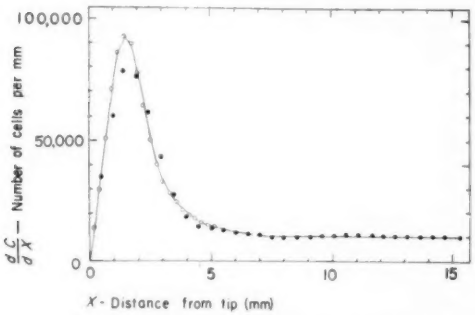

FIG. 6. Smoothed values of linear cell density. Open circles are values calculated from smaller histogram (0.5-mm.) of figure 2; closed circles, from larger histogram (3-mm.).

proportional to $\Delta C/\Delta X$. The area of each bar is then proportional to ΔC, or, in terms of the dC/dX curve which is desired, to the definite integral $\int_{X_1}^{X_2}(dC/dX)dX$, where X_1 and X_2 are the two ends of the segment. It is apparent then that values of dC/dX for each segment should be estimated so that their integral from X_1 to X_2 equals ΔC, the number of cells in that segment. Any number of curves representing dC/dX could be found which would fulfill this requirement. Hence, it seems reasonable to make a second requirement, that the dC/dX curve be as smooth as is consistent with the first requirement.

On the basis of these considerations the following method has been used to derive the smooth curve shown in figure 6, by successive approximations. A curve was first drawn by eye to approximate the area of the 0.5-mm. histogram (fig. 2), and preliminary values of dC/dX were read from this curve at each nominal 0.25-mm. point. Any values whatever might have been used, but calculating time is saved by making the first approximation as accurate as possible. Areas under portions of this preliminary curve corresponding to each histogram bar were then calculated by Simpson's rule for numerical integration (Milne, 1949). The ratio of the area of each histogram bar to the corresponding area under the curve was found, and each preliminary value multiplied by the appropriate ratio to reconcile the two areas. The 7-point cubic smoothing formula (Milne, 1949) was applied to these adjusted values, and the area under each portion of the new curve again reconciled with the area of the corresponding histogram bar. By repetition of this alternate smoothing and adjustment of area under the curve, series of dC/dX values were obtained which fulfilled more and more closely the two requirements laid down. Four repetitions of the process were judged to be adequate. In estimating dC/dX values at each nominal 0.5-mm. point from the 3-mm. data, the smoothed values from the 0.5-mm. counts were used as preliminary values in the first 5 mm., and values were taken from a line fitted to the histogram by eye at greater distances from the tip. Two repetitions of the integrating and smoothing process appeared to be adequate. The two sets of data appear to be in satisfactory agreement.

This calculation has been carried out as though the segments were precisely 0.5 mm. and 3.0 mm. long. In both cases the cutting jig provides segments which average somewhat longer than the nominal lengths, and which vary somewhat from one segment to another (table 1). Since the values to which the smoothing and integration formulas have been applied are not equally spaced along the X-axis, some error is introduced by the iteration process.

In order to reconcile the 0.5-mm. and 3-mm. data, the smoothed dC/dX values were plotted against the true X-values in a large scale graph similar to figure 6. By graphical interpolation a value of dC/dX was read at each 0.25 mm. of true root length, to correspond with values of dX/dt obtained from the growth studies (Erickson and Sax, 1956). In the first 3 mm. from the tip, the interpolation was based entirely on the 0.5-mm. segments, and beyond 8 mm., dC/dX was taken as constant. Between 3 mm. and 8 mm., values were read from a smooth curve drawn by eye as a compromise between the two sets of data.

RATE OF CELL FORMATION

In order to estimate the hourly rate of cell formation by an apical segment, dC/dt, these values of dC/dX were multiplied by corresponding dX/dt values obtained from the growth studies (Erickson and Sax, 1956, table 1). The resulting curve for the most part fluctuated meaninglessly, indicating that the growth data and the cell number data were not consistent. The growth analysis was based on 10 photographic records which were selected from a larger number, and the cell counts were made from roots chosen for straightness from trays containing large numbers of seedlings. Unfortunately,

TABLE 4

SMOOTHED VALUES OF RATES OF CHANGE OF CELL NUMBER, ETC.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
0.00	0.000	0.000	0	0	0	0	0.000	0	0.000	44		0.000	
.25	.001	.011	15,000	15,000	15	15	.013	362	.008	37	24	−0.001	0.000
.50	.008	.034	34,800	34,800	278	278	.056	1,400	.018	28	40	.008	−0.002
.75	.016	.058	54,400	54,400	870	870	.088	2,080	.016	20	38	.015	.008
1.00	.039	.091	73,000	73,000	2,850	2,850	.127	2,220	.009	18	30	.004	.028
.25	.061	.119	87,200	87,200	5,320	5,320	.145	2,330	.001	20	27	+0.031	.032
.50	.099	.152	92,700	92,700	9,180	9,180	.154	2,330	.000	24	25	.074	+0.010
.75	.137	.189	89,700	89,700	12,290	12,290	.142	"	"	28	26	.120	.044
2.00	.194	.233	79,600	79,600	15,440	15,440	.107			35	29	.150	.130
.25	.253	.278	65,700	65,700	16,620	16,620	.068			43	36	.172	.214
.50	.333	.319	52,300	52,300	17,420	17,420	.023			49	45	.200	.298
.75	.413	.356	41,600	42,370	17,180	17,500	.007			57	55	.236	.348
3.00	.509	.382	34,700	34,380	17,660	"	.000			66	68	.279	.385
.25	.604	.402	29,500	28,970	17,820		"			75	80	.333	.403
.50	.709	.406	25,600	24,680	18,150					86	94	.425	.406
.75	.807	.400	22,700	21,690	18,320					101	107	.456	.400
4.00	.908	.390	20,100	19,270	18,250					116	121	.473	.391
.25	1.001	.378	17,900	17,480	17,920					131	133	.477	.379
.50	.098	.366	16,400	15,940	18,010						146		.365
.75	.183	.348	15,300	14,790	18,100						158		.348
5.00	.272	.328	14,400	13,760	18,320						169		.329
.25	.347	.304	13,700	12,990	18,450						179		.305
.50	.424	.281	13,100	12,290	18,650						190		.281
.75	.487	.258	12,600	11,770	18,740						198		.258
6.00	.553	.229	12,200	11,270	18,950						207		.229
.25	.602	.199	11,800	10,920	18,900						213		.198
.50	.650	.156	11,400	10,610	18,810						220		.155
.75	.683	.120	11,000	10,400	18,510						224		.120
7.00	.708	.082	10,600	10,250	18,100						227		.085
.25	.725	.057	10,300	10,140	17,770						230		.060
.50	.737	.037	10,100	10,070	17,540						231		.038
.75	.744	.021	10,000	10,030	17,440						232		.019
8.00	.748	.010	10,000	10,010	17,480						233		.008
.25	.749	.004	"	10,010	17,490						233		.003
.50	.750	.001		10,000	17,500						"		.001
.75	.750	.000		"	"								.000
9.00	"	"											

Column Headings:

(1) X—Distance from tip of root (mm.).
(2) dX/dt—Mean rate of displacement of marks from tip (mm.·hr.$^{-1}$). From records selected to be consistent with cell counts.
(3) $d(dX/dt)/dX$—Relative elemental rate of elongation (hr.$^{-1}$). Calculated from (2).
(4) dC/dX—Linear cell density (cells·mm.$^{-1}$). Estimated from counts of table 2.
(5) dC/dX—Linear cell density adjusted to constant value beyond 2.75 mm. from tip.
(6) dC/dt—Rate of cell formation by an apical segment (cells·hr.$^{-1}$). Calculated from (2) and (4).
(7) dC/dt—Rate of cell formation. Calculated from (2) and (5).
(8) $d(dC/dt)/dC$—Relative elemental rate of cell formation (hr.$^{-1}$). Calculated from (7).
(9) F_c—Number of transverse files of cells. Estimated from data of figure 3.
(10) $(dF_c/dt)/F_c$—Relative rate of change of number of files (hr.$^{-1}$). Calculated from (9).
(11) L_c—Mean cell lengths (μ). Estimated from measurements of figure 4.
(12) L_c—Mean cell lengths estimated from other data by means of formula (8).
(13) $(dL_c/dt)/L_c$—Relative rate of cell elongation (hr.$^{-1}$). Calculated from (11).
(14) $(dL_c/dt)/L_c$—Relative rate of cell elongation. Calculated from (12).

no growth measurements were made of the latter, but it is probable that the roots used for the growth analysis were growing at a more rapid overall rate than those used for estimating cell numbers. Five of the 10 growth records were selected, which gave a lower overall growth rate,

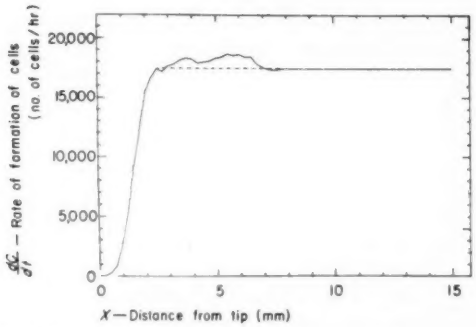

FIG. 7. Rate of formation of cells by an apical segment. See text for derivation.

1.75 mm.·hr.$^{-1}$, and dX/dt was estimated at each 0.25 mm. from these (table 4, col. 2). When these values were multiplied by the dC/dX values derived as above (table 4, col. 4), the dC/dt curve shown as a solid line in figure 7 was obtained. Fluctuations are still present between 2.5 and 7.5 mm., but it appears that the rate of cell formation by an apical portion of the root rises from 0 at the tip to 17,000–19,000 cells·hr.$^{-1}$ at 2.5 mm. and greater distances from the tip.

The counts of mitotic stages demonstrated that cell divisions do not occur beyond 2.5 mm. from the tip. Therefore, one should expect that the rate of cell formation by an apical segment, dC/dt, is constant for apical segments longer than 2.5 mm. Accordingly, the dashed line has been drawn in figure 7 at 17,500 cells·hr.$^{-1}$, the value obtained at values of X greater than 8 mm. Dividing the values of dC/dt represented by this line by the dX/dt values gives a new set of dC/dX values which are listed in table 4, column 5. They differ little from those obtained more directly from the counts, and appear to be quite within the confidence limits about the counts. They are used in all the subsequent calculations.

RELATIVE ELEMENTAL RATE OF CELL FORMATION

From the dC/dt values (table 4, col. 7) the relative elemental rate was calculated by applying the 7-point derivative formula, to give $d(dC/dt)/dX$, at each 0.25 mm., and dividing each of these by corresponding dC/dX. The resulting rates are listed in table 4, column 8, and are plotted as a dotted line in figure 8. It will be seen that the relative elemental rate of cell formation is at a maximum of about 0.16 hr.$^{-1}$ at 1.25 mm. from the tip of the root.

RELATIVE RATE OF CHANGE OF NUMBER OF FILES

The transverse sections from which counts of number of files of cells were made were spaced irregularly along the root axis. In order to derive a value of F_c for each 0.25 mm. of root length, a smoothing procedure based on fitting of parabolic arcs to successive groups of points was used. The smoothed values are listed in table 4, column 9, and shown as an unbroken line in figure 3. Application of the 7-point derivative formula to these values yields estimates of dF_c/dX, the rate of change of number of files with length, and multiplication of this by dX/dt and division by F_c gives the desired relative rate, $(dF_c/dt)/F_c$. This rate corresponds approximately to the rate of cell division in planes parallel to the root axis. It has its maximum of 0.01 hr.$^{-1}$ at about 0.5 mm. from the tip of the root cap, and is zero at the point, 1.25 mm. from the tip, where the rate of cell divisions in all planes, $d(dC/dt)/dC$, is at a maximum. This curve has been plotted below the X-axis in figure 8, since it enters formula (9) as a negative term.

RELATIVE RATE OF CELL ELONGATION

As stated above, means of cell length measurements are plotted in figure 5 as points and as a solid line for the first 4.5 mm. of root length. Since dC/dX and F_c are known, cell lengths, L_c,

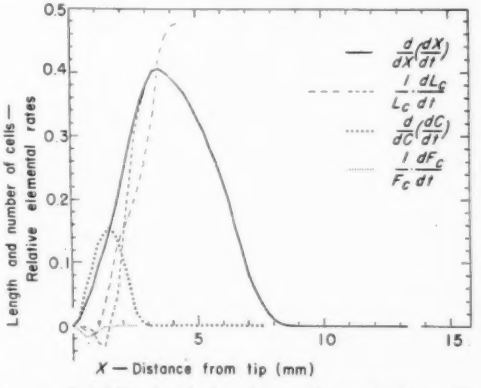

FIG. 8. Solid line is relative elemental rate of elongation; larger dots, relative elemental rate of cell formation; smaller dots, relative rate of change of number of files of cells; longer dashes, relative rate of cell elongation, calculated from measured cell lengths of figure 4; shorter dashes, relative rate of cell elongation, obtained by difference from first 3 rates.

can also be estimated indirectly as shown by formula (8). On cancelling dt and rearranging terms, this formula becomes $L_e = F_e(dX/dC)$. Cell lengths calculated from this formula are listed in table 4, column 12, and are plotted in figure 5 as a dashed line. The indirect estimates are in satisfactory agreement with the measurements of cell length, as far as they go. Mean cell lengths appear to be at a minimum of about 20 μ at 1.0–1.5 mm. from the tip, and reach a limiting value of 233 μ at about 8 mm. from the tip.

The relative rate of cell elongation was obtained by applying the 7-point derivative formula to the values of L_e to obtain dL_e/dX, multiplying by dX/dt, and dividing by L_e, just as was done for number of files. Two versions of this relative rate were calculated, one derived from the measured cell lengths (longer dashes in figure 8), and the other from the indirectly estimated lengths (shorter dashes in figure 8). In the first 1.0–1.5 mm. of the root, mean cell length is decreasing at rates as great as 0.01 to 0.02 hr.$^{-1}$. This, of course, is brought about by division of the cells. At greater distances from the tip, the relative rate of cell elongation increases, until at 3 mm. and greater distances from the tip, where cell division has ceased, it equals the relative elemental rate of elongation of the root.

DISCUSSION

It is apparent from figures 4 and 7 that cell divisions occur only within the apical 2.5 mm. of the root, and that the overall rate is about 17,500 cells·hr.$^{-1}$. Besides the rate at which cells are being produced by the root as a whole, two other conclusions may be drawn from these data.

Following the reasoning presented in the previous paper (Erickson and Sax, 1956: 24 and footnote 4) concerning dX/dt, dC/dt may be taken as proportional to dC, the number of cells comprising an element of the root. It is then interesting to compare this elemental number of cells at the meristematic apex with that in the mature portion of the root. The apex of the meristem is very nearly at 0.5 mm. from the tip, and at this point dC/dt is estimated at 278 cells·hr.$^{-1}$. Beyond 2.5 mm. from the tip dC/dt is taken as 17,500 cells·hr.$^{-1}$. The ratio of the latter to the former is 63, and, since this is very nearly 2^6, it may be concluded that, on the average, meristematic initial cells go through 6 cycles of mitotic division before ceasing to divide. It must be stressed that this is an average value. We have preliminary data which indicate that there are differences in the number of cell generations involved in formation of the different mature cell types of the root.

It is also possible to plot a growth curve for an element of cell number in the same manner as was done for an element of length. It is evident from this graph of dC/dt vs. t (fig. 9, solid line) and of log (dC/dt) vs. t (broken line) that the growth curve is neither exponential in its early part nor symmetrically sigmoid as a whole. There is a prolonged lag phase, followed by a rapid rise and a sudden levelling off as cell divisions cease. In other words, the growth in cell number of an element of the root does not, for instance, have the characteristics of growth in cell number of a culture of microorganisms. These same characteristics of growth in cell number are shown in derivative form by plotting $d(dC/dt)/dC$ against X (fig. 8) or against t. It is apparent, for instance, that the relative elemental rate of cell division is not constant as would be required for exponential growth, but rises to a maximum of 0.16 hr.$^{-1}$ and then decreases with increasing distance from the tip.

From figure 9 one may also form an estimate of the average duration of the mitotic cycle, or the generation time of the meristematic cells in various portions of the meristem. This may be done by noting the times at which successive doublings of dC/dt, or unit increments of $\log_2 (dC/dt)$, have occurred. Beginning at the point which corresponds to the meristematic apex at 0.5 mm. from the tip, these times have been estimated by Aitken's method of interpolation from values of $\log_2 (dC/dt)$, and are indicated by arrows in figure 9. The time intervals

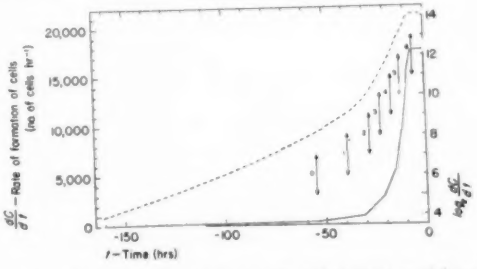

FIG. 9. Rate of formation of cells (solid line) and logarithm of this rate (dashes) as a function of time. Arrows indicate successive doublings of elemental cell number.

for the 6 successive doublings of elemental cell number are estimated as 15.8, 10.8, 5.5, 4.4, and 6.6 hrs., respectively. The accuracy of these estimates is probably not great because of the limitations of our data, and uncertainties involved in smoothing, but it is undoubtedly true that the duration of mitosis decreases with increasing distance from the meristematic apex. In the apical part of the meristem, it may be that all of the cells are dividing. If this is so, the average duration estimated in this way probably corresponds to the actual duration of division in each cell. In the basal part of the meristem, however, it is probable that many cells have ceased dividing. In this case, the actual duration of mitosis in those cells which are dividing is probably considerably shorter, and they go through more cycles of division, than our estimated average durations indicate. A more penetrating analysis is required to clarify this point.

In considering the interrelationship of cell division and cell elongation in the root, it may be advantageous to picture a hypothetical group of cells which are dividing at a constant mean relative rate, i.e., exponentially, and which are elongating at the same relative rate. If the divisions occurred randomly in time, their mean cell length would be constant with time. If, however, the relative rates of elongation and of cell division were to differ, a change in mean length with time would ensue.

It is clear from figures 5 and 8 that the latter is the case within the meristematic region of the root. Ignoring the changes in number of files of cells, one can conclude in broad terms that the relative rate of change in cell number exceeds that of elongation in the first 1.25 mm., and there is consequently a decrease in mean cell length, as seen in figure 5, and a negative rate of change in cell length, shown in figure 8. Between 1.25 and 2.5 mm., the mitotic rate drops below the relative elemental rate of elongation, and the mean cell length increases.

Basal to the meristematic region, the relative rate of increase in mean cell length is identical with the relative rate of increase in length of an element, i.e., the growth in length of portions of the root is wholly due to the growth of its constituent cells. By plotting L_e vs. t, a cell growth curve could be obtained. Beyond 2.5 mm. from the tip, this curve is identical in form with that of dX/dt vs. t (Erickson and Sax, 1956: fig. 9) and, as pointed out there, it departs markedly from the theoretical exponential and autocatalytic analogies.

Among the numerous studies of root growth which have been made since Sachs' (1873) time, there are very few which yield even rough estimates of the time rates of cell division and cell elongation. In botany textbooks and treatises, the growing portion of a root is usually described as consisting of several regions or zones: (1) the root cap, the cells of which are formed by a basal calyptrogen, (2) the meristematic region, the cells of which are dividing mitotically, and are usually said to be elongating to keep pace with their division, (3) the region of elongation, and (4) the region of maturation. The recognition of these zones has been based almost solely on examination of longitudinal microtome sections of the root. For instance, the meristematic region is recognized by the presence of mitotic figures, and the region of elongation by the appearance of a progressive increase in cell length with increasing distance from the tip. Such verbal descriptions of the root, of course, fail to convey any idea of the quantitative relationships among the processes going on in the root.

Among relatively recent studies of growing roots, in which efforts have been made to follow cellular changes with time, is Sinnott and Bloch's (1939) work on *Phleum pratense*. They have published camera lucida drawings of epidermal cells, in which the progressive elongation and division of cells may be seen. However, they made no attempts to calculate rates of division and elongation, and, unfortunately for such a calculation, they do not indicate unequivocally the position of the cells drawn with respect to the root apex. This study of the *Phleum* root was continued by Brumfield (1942) using a photographic method of recording cell lengths. He made an effort to work out rates of cell elongation, but used a rather crude method of analysis. It is difficult, for instance, to see in his figure 4 any evidence for his conclusion that the root is divided into discrete zones, within which the percentage rate of cell elongation is constant (fig. 6). Rather, the relative growth rates of the cell complexes shown in his figures appear to be changing continuously with time, as we have found. Brumfield was able to draw the qualitative conclusion that "cells near the tip undergo more division than those farther behind it," but his data, largely confined to one root, do not allow any estimate of rates of mitosis in various portions of the root.

Goodwin and Stepka (1945) used a device consisting of a swinging mirror attached to the stage of a microscope, with a lamp and scale, for measuring the rates of displacement of cells from the tip of the *Phleum* root, and subjected their data to a more careful analysis than Brumfield's. Measurements of lengths of epidermal cells were used with the growth data to derive rates of formation of new transverse cell walls, which are equivalent to mitotic rates. Qualitatively, their conclusions about the pattern of elongation are similar to ours, but they have quoted a much higher relative elemental rate of elongation, about 1.27 $hr.^{-1}$, than occurs in the corn root. While their method of deriving rates appears valid to us, they have reached the conclusion that the maximum rate of cell formation and of cell elongation both occur at the same distance, 0.4 mm., from the tip of the root. In the corn root, these two maxima do not coincide, cell division having ceased at the point where elongation is proceeding most rapidly. This discrepancy may be due to the small number of roots which they studied, or to a discrepancy in growth rate between the roots used for the growth data and those which provided the cell length data as a function of root length. Our data suffer from a similar defect (p. 16).

Baldovinos (1954) has made growth studies on roots of *Zea mays* by placing marks at 1-mm. intervals from the tip and measuring the distances between marks at 3-hr. intervals. He reports that elongation occurs only within the first 4 mm. from the tip, while we find that the growing zone is 8–10 mm. long. It is probable that he has underestimated its length by his relatively insensitive method of measurement, particularly since he shows that cell length is increasing up to 5 mm. from the tip. He finds that elongation is greatest between marks which were initially 1 and 2 mm. from the tip, whereas we find the most rapid elongation at about 4 mm. from the tip. This discrepancy is partly explained by his technique. The classical marking technique tends to overestimate the maximum growth rate, and to displace the maximum toward the tip. These errors are greater the longer the times between measurements. They are great enough even after one hour to make methods of estimating instantaneous rates, such as are described here, highly desirable. Baldovinos has measured the lengths of cortical cells, and from these data calculated the average "number of cells per mm." in one file of the cortex. From these and his growth data he has made estimates of the specific rate of cell division in each segment. While his specific rate corresponds to the relative rates we have calculated, he quotes a much smaller rate for cell division than we have found. However, direct comparisons are difficult, since he has not determined the number of files of cells, and hence has no estimate of the total number of cells in each segment.

Burström (1941, 1947) has described methods for estimating rates of cell division and cell elongation in excised wheat roots grown in nutrient solutions. Rates are calculated from measurements of total length of the root segment, length of meristem, mean length of mature epidermal cells and meristematic epidermal cells, made at the start and at the end of a 5- to 15-day period of growth. He has used these methods and modifications of them in a series of studies assessing the effect of nutrients, temperature, osmotic pressure, and of growth-promoting and growth-inhibiting substances on root growth (Burström, 1949–1954, and other papers). Burström's experiments are of fairly long duration, and the rates which he has calculated have to do with the behavior of the whole excised root. They do not yield information on the topic of the present study, the instantaneous rates at which cell division and elongation occur at various points along the root. Furthermore, his observations are largely confined to the epidermal cells, as are those of Sinnott and Bloch, Brumfield, and Goodwin and Stepka. In calculating the "rate of total cell divisions per day," R_d, he has multiplied the rate of division in an epidermal cell file by an estimate of the total number of files of cells in the root. This procedure implies an assumption that the pattern of cell division and elongation for various types of cells within the root are similar to those for the epidermis. This is a subject on which no precise information has been published.

Brown and Rickless (1949) introduced a technique for macerating roots and making hemocytometer counts of the resulting cell suspensions, in their study of the growth of excised apical segments of *Cucurbita pepo* roots. In parallel samples of segments withdrawn from the culture solution at 12-hr. intervals, they have determined the mean length of segments, number of meristematic ("non-vacuolate") cells, and number of vacuolate cells. From these data they have estimated rates of cell division and of cell elongation. The initial length of segments

was 1.6 mm., and the segments were estimated to contain an average of 67,300 cells. This may be compared with the corn root, in which the apical 1.6 mm. has about 85,000 cells. In all their experiments the rate of cell formation falls off with time, but the initial rate may be compared with that in the intact corn root. At 25° C., in a medium containing salts, sucrose, and yeast extract, the increment in cell number over the first 12 hrs. was 47,700, giving an average rate of nearly 4,000 cells·hr.$^{-1}$. Numerical differentiation of these data (table 3) yields a somewhat higher estimate of the initial rate, 5,100 cells·hr.$^{-1}$, but this also is considerably lower than the rate of 17,500 cells·hr.$^{-1}$ for the intact corn root. Brown and Rickless also present data on the elongation of these apical segments. The greatest increment in length over a 12-hr. period shown in their table 7 is 4.0 mm., giving an average rate of 0.33 mm.·hr.$^{-1}$. Since the segments did not include the region in which elongation is most rapid in the intact root, it is difficult to make comparisons with our data. In later papers, Brown, Robinson, and Johnson (1949), and Brown and Sutcliffe (1950) have studied the elongation of excised segments in greater detail. In the latter paper, the most rapid growth reported is for a segment 1.5 to 3.0 mm. from the tip, in 20 per cent sucrose in the presence of potassium at 25° C. (table 3). We calculate that the average relative rate of growth over the first 4 hrs. of this experiment is about 0.10 hr.$^{-1}$. They give no data on the growth of this region in the intact *Cucurbita* root, but our data indicate that in corn the region from 1.5 to 3.0 mm. has an instantaneous relative rate of elongation of 0.22 hr.$^{-1}$. Two uncertainties are involved in making these comparisons, the difference in species of plant used and the fact that Brown and his collaborators have studied excised root segments, whereas our work pertains to intact roots.

The data published by Brown and his collaborators pertaining to the growth of portions or elements of the root are limited. However, it is gratifying to find that Brown and Broadbent's (1950) data on number of cells in segments of pea roots are in good agreement with ours on the corn root. From their table 1, we estimate that the linear cell density, dC/dX, is at a maximum of 98,000 cells·mm.$^{-1}$ at about 0.9 mm. from the tip, and that beyond 4.5 mm., where elongation has presumably ceased, it comes to a constant value of 12,300 cells·mm.$^{-1}$. The ratio of these two values is about 8. In the corn root, the corresponding values are 95,000 and 10,000, with a ratio of 9.5. Whether the difference in length of the growing portion of the pea and corn roots is correlated with their differing histogenic organization (Janczewski, 1874) is an interesting subject for speculation. Wanner (1950) has presented cell counts on *Allium* roots which are also consistent with Brown and Broadbent's and our data, though the gradual decrease in number of cells from 4 to 10 mm. shown in his figure 4 is hard to understand. Reid's (1941) more limited data on cowpea (*Vigna sinensis?*) roots indicate 128,000 cells in the region from about 0.2 to 1.2 mm. from the tip of the root cap. The maximum linear cell density, dC/dX, must therefore be considerably higher than 128,000 cells·mm.$^{-1}$, and, since she estimates 9,300 cells·mm.$^{-1}$ beyond 5.2 mm., one would conclude that the ratio of maximum cell density to that of older portions of the root is very much higher than 8 or 10 found by Brown and Broadbent, Wanner and us. It is probable that the methods used by Wanner and Reid (and by others for other plant organs) for estimating cell numbers from measurements of microtome sections have greater inherent errors than maceration techniques.

Gray and Scholes (1951), in their study of the effect of irradiation on roots of *Vicia faba*, have developed mathematical methods which are similar to ours. Their formula (1), $M = (Z/L)g$, is identical to our formula (8), $dC/dt = (F_c/L_c) \times (dX/dt)$, in the case where dX/dt is taken as the overall rate of elongation of the root, dC/dt as the rate of cell formation by the root as a whole, and F_c and L_c are taken basal to the growing region. Gray and Scholes have not systematically formulated the varying rates of cell formation and cell elongation along the axis of the root, though they are aware of this problem, and have plotted average cell lengths (figs. 4, 20) and percentages of cells in mitosis (figs. 5, 15, 18) as functions of distance from the tip. On the other hand, they have developed mathematical methods for dealing with changes of the growth pattern with time, and have amply demonstrated that such methods are essential to the interpretation of results of experimental treatment of the root.

Since Gray and Scholes' approach is so nearly the same as ours, it is of especial interest to compare their data on control roots of *Vicia* with ours on *Zea*. From their table 4, the overall rate of elongation, g, is 0.86 mm.·hr.$^{-1}$, at 19° C.,

the number of cells in transverse section basal to the meristem, Z, is 1,890, and the mean length of fully elongated cells, L, is 0.156 mm., from which the rate of cell formation, M, is calculated as 10,400 cells·hr.$^{-1}$. The corresponding values for *Zea* at 25° C. are 1.75 mm.·hr.$^{-1}$, 2,300, 0.160 mm., and 17,500 cells·hr.$^{-1}$.

Mitotic counts in the meristematic region of the root have been made frequently, in both descriptive and experimental studies. In some cases, all cells in each sample have been scored for their mitotic stage, as in Brown's (1951) study of temperature effects on cell division, and in the data represented by figure 4 above.[2] The results of such counts are expressed as the ratio or percentage of cells at specified stages, usually prophase, metaphase, anaphase, and telophase, to the total number of cells in a sample. Such a ratio is termed a mitotic index. In other cases, only cells in specified stages have been counted, and referred to an arbitrary mass of meristematic tissue, or to an arbitrary portion of a microtome section (e.g., Wagner, 1930, 1937; Erickson and Rosen, 1949). A large amount of data on roots of these two kinds has been accumulated in connection with studies of diurnal mitotic rhythms (e.g., Kellicott, 1904; Friesner, 1920); of the effects of radiation (Gray and Scholes, 1951); and of mitotic inhibitors. Mitotic counts on sectioned roots had a central part in the controversy over the existence of mitogenetic radiation, and were cited by both the proponents (Gurwitsch, 1929) and the opponents (Guttenberg, 1928; Taylor and Harvey, 1931) of this notion.

A mitotic index should not be mistaken for a mitotic rate. Although many authors appear to make the tacit assumption that the mitotic index within a tissue is proportional to the time rate at which cell divisions are occurring, it is actually only indicative of the proportion of the whole mitotic cycle occupied by the specified stages. A mitotic index may be interpreted as the relative duration of the stages to which it refers, provided that it can be shown that the cells observed were dividing randomly, continuously, and without change of average rate, at the moment of fixation. To calculate the absolute durations of various stages from their relative durations, the length of the entire mitotic cycle must be known. If this is known, a mitotic rate can also be calculated. It is in the nature of the case that no conclusion can be drawn about the time rate at which a process occurs within a tissue simply from observations of a sectioned or smeared preparation which was killed at a given instant of time. Some supplementary observations which can be related to time are necessary to allow conclusions about time rates of mitosis to be drawn from mitotic index data.

Laughlin (1919) has explored this question quite thoroughly in the case of the *Allium* root. He grew onion roots at three constant temperatures, with daily periods of darkness and light from a north window. Under these conditions there is a diurnal fluctuation of the mitotic index with a maximum at about noon and another during the night. On one day he fixed roots at 10-min. intervals from 10 A.M. to 1 P.M., embracing one mitotic index maximum. He prepared stained sections and scored cells in random portions of the sections for ten arbitrarily defined "active" stages of mitosis, and interphase. These data gave estimates of the mitotic index and stage index (no. of cells at a given stage)/(no. of "active" cells), for each time and temperature. He also calculated "procession indices," which are stage indices corrected for variations in sample size, mitotic index, and average relative duration of each stage. By entering these indices in a 2-way table under stage and sampling time, and tracing maxima of the index through stages and times, he arrived at average absolute durations for each stage, and for the "active" portion of the mitotic cycle. From these durations at each of three temperatures, he estimated temperature coefficients for each stage.

In Laughlin's work, the necessity for making supplementary observations related to time, in interpreting mitotic index data, is met by sampling at close intervals during a mitotic index maximum. He states explicitly (p. 10) that his method would fail if the mitotic index were constant. He apparently has not taken into account variations of mitotic index (Wagner, 1930, 1937) and mitotic rate (fig. 4 above) with distance from the tip of the root. This variation must constitute a large part of the variance of his counts. One may also question the reality of the peaks of the procession index which he has traced in tables 12–14. They appear much more clearly

[2] We understand interphase to be a mitotic stage, although Brown and some other authors make a distinction between interphase and the "mitotic" stages, prophase, metaphase, anaphase, and telophase. A logical distinction may be made between the interphase which intervenes between telophase and the following prophase, and the "terminal interphase" of a cell which is destined not to divide again. The microscopic distinction, however, is difficult.

in his preliminary study under diurnal temperature fluctuations.

Brown (1951) has applied his maceration technique to the problem of estimating the duration of the mitotic cycle in pea roots. In paired samples of roots, he excised the apical 5.0 mm. in one sample and in the other placed marks at 5.0 mm. from the tip and allowed them to grow for 24 hrs., whereupon he removed the marked apical portion. Macerations and cell counts were made on both groups of segments, and the increment in cell number over 24 hrs. was found. This increment divided by the number of "non-vacuolate" cells gave a rate of division and an average duration of mitosis. From smear preparations of other samples of roots, the percentages of cells in various stages of division, mitotic indices, were determined. From these data the duration of each stage was calculated. These determinations were made at four temperatures, and temperature coefficients were calculated. The direct method used by Brown to determine the length of the mitotic cycle has much to recommend it. However, it yields no information about the varying rates of cell division along the axis of the root, and there may be some question about the validity of the estimation of an average duration of mitosis for cells which differ as greatly in their rate of division as do those of the root.

SUMMARY

Primary roots of *Zea mays* seedlings have been cut into successive segments beginning at the tip. From macerations and microtome sections of these segments, estimates have been made of cell number, average cell length, number of cells in cross section, and mitotic index in each segment. From these data and growth data obtained in a previous study, time rates of change of each of these quantities at each point along the root have been found. These rates, and, more particularly, the equation relating them to each other, constitute a quantitative analysis of root growth in morphological terms. From this equation, $d(dX/dt)/dX = [d(dC/dt)/dC - (dF_c/dt)/F_c] + (dL_c/dt)/L_c$, it is apparent that the relative elemental rate of elongation at each point along the root is equal to the relative elemental rate of cell division, minus the relative rate of change in number of files of cells, plus the relative rate of cell elongation. The relative elemental rate of cell formation, $d(dC/dt)/dC$, rises to a maximum of about 0.16 hr.$^{-1}$ at about 1.25 mm. from the tip, and declines to zero at about 2.5 mm. The relative rate of change in number of files, $(dF_c/dt)/F_c$, corresponding to those cell divisions which are not transverse to the axis, has a much smaller maximum of 0.01 hr.$^{-1}$ at about 0.5 mm. from the tip. The relative rate of change of mean cell length, $(dL_c/dt)/L_c$, has negative values in the first 1.0 to 1.5 mm. of the root, but increases until at 2.5 to 3.0 mm. and greater distances from the tip, where cell division has ceased, it is identical with the relative elemental rate of elongation, $d(dX/dt)/dX$. That is to say, it has a maximum of nearly 0.40 hr.$^{-1}$ at about 4 mm., and decreases to zero at 8 to 10 mm. from the tip.

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THE "LANGUAGE" AND ORIENTATION OF THE BEES

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(*Read by Donald R. Griffin, Harvard University, April 20, 1956*)

In a bee hive (Bienenstaat) there is in force a well-organized division of labor. While the young worker bees care for the domestic affairs, the care of the brood and comb construction, the older bees fly out to collect nectar and pollen to feed the colony. There is a further division of labor among the collecting bees. In the first place, only a very few bees, the scouts, fly out independently to discover new sources of food. Most of the bees wait in the hive until they receive directions to make their way to a particular goal. Secondly, the assemblage of collecting bees is divided into working groups each of which seeks out one particular kind of flower. The size of the working groups is proportional to the productivity of the available flowers. At any given time the largest group of bees will be at the flowers where the best crop is available. This is all very sensible; but how is it possible?

A scout bee may find a good source of food near the home hive—it can be a flower with pollen or nectar or, in an experiment, a glass dish with sugar water. When the scout returns to the hive, she performs a round dance on the comb (fig. 1). This dance indicates symbolically to her hivemates that they should fly out and search around the hive. Inactive bees sitting near the dancer are thus aroused and stimulated to fly out. While they are still trooping after the dancer on the honeycomb, touching her with their antennae which bear the olfactory organs, they learn the kind of flowers for which they must search. Every species of flower has a specific odor. It clings to the scout bee which has collected from the flower, and it clings also to the nectar which she feeds the bees surrounding her during slight hesitations in her dance. The new collectors search for this odor and thus succeed in finding the correct goal. They too dance upon returning to the hive and after all subsequent collecting flights for as long as they find an abundant food supply. In this way the worker group becomes larger and larger as long as it is successful.

The liveliness and duration of any one of these dances depend on the sweetness and quantity of the nectar which the bee has found during the preceding collecting flight. The larger the helpings at the restaurant thus patronized, so to speak, the livelier the dance; the livelier the dance, the more new bees are attracted. And so the size of the worker group for each of the plants blooming at one time is regulated relative to the yield of the flowers.

If the species of flower discovered in this way is more than 50 or 100 meters from the hive, then the round dance is supplanted by the "wagging" dance (Schwänzeltanz) (fig. 1). The bee now moves in a straight line while wagging her abdomen vigorously; then she runs in a half-circle back to the starting point, and again the wagging course (Schwänzellauf), then a half-circle to the other side, and so forth. The wagging dance means, like the round dance, that there is something to fetch outside. The flower species is identified by its odor, and the available yield through the spirit and duration of the dance. But in addition, this dance form conveys information

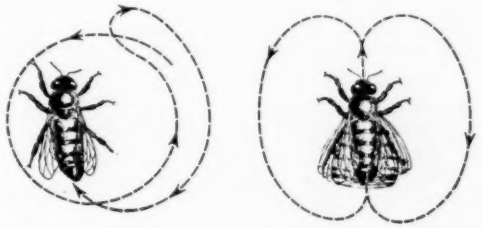

Fig. 1. Round dance (left) and wagging dance (right) of the bee. From K. v. Frisch, Sprechende Tänze im Bienenvolk, München, 1955.

* On November 11, 1955, the Society in Executive Session voted to award the Magellanic Premium to Dr. von Frisch in recognition of his studies of animal sense organs and his analysis of the dances of bees. The Magellanic Medal was presented to Mr. Horst Pelckmann, First Secretary to the German Embassy, on behalf of Dr. von Frisch on April 20, 1956.

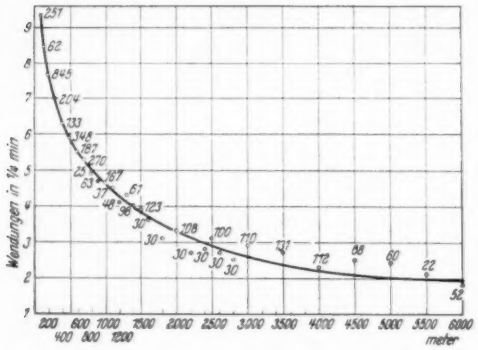

FIG. 2. The expression of distance by bees. Abscissa: distance of the feeding place from bee hive in meters, ordinate: number of wagging runs per quarter minute. The points on the curve are average values; the accompanying figures give the number of single observations. From K. v. Frisch, Sprechende Tänze im Bienenvolk, München, 1955.

about the distance to the goal and about the direction in which it lies.

The distance of the feeding area is shown by the rhythm of the dance. The more distant the food, the more slowly the turns of the dance follow one another, the fewer wagging courses occur therefore in a given time (fig. 2).

The direction of the Schwänzellauf conveys the direction of the goal, with reference to the position of the sun. This point is most clearly seen when the dance takes place on a horizontal surface and under a clear sky. One can observe it under these conditions if in warm weather part of the bee population loiters on the landing board just outside the hive entrance and some of the homecoming bees stop here to give up their load and to dance. They orient themselves in such a way that during the wagging course the sun is seen on the same side and at the same angle to their path as was the case on their flight to the feeding place. They thus point directly to the goal (fig. 3). The bees which troop after the dancing scout bees perceive this relationship relative to the sun, and since they assume this same position on flying out, they fly in the direction of the goal.

Most of the time, however, the returning bees dance inside the pitch-dark hive—on the vertical honeycomb. Then the angle to the sun's position is translated into an angle relative to the force of gravity according to the following rule: The direction toward the sun is indicated by a wagging course straight up. A direction 60° left of the sun is rendered by a wagging course 60° to the left of the upward direction, and so forth (fig. 4). It has been possible to show experimentally that bees which are aroused by the dances on the honeycombs and fly out to the food hold very exactly to the distance- and direction-data imparted to them.

To indicate direction in this way it is necessary to know the sun's position. What do the bees do when the sky is cloudy? The answer is as simple as it is surprising: they see the sun through a complete cloud cover. This can be demonstrated when one lays the observation hive on its side. On the horizontal surface the dancers orient their wagging course directly toward the goal. Under a cloudy sky they show the correct direction if they have a free view of that portion of the sky where, invisible to us, the sun stands behind the clouds, but their dances are completely disoriented

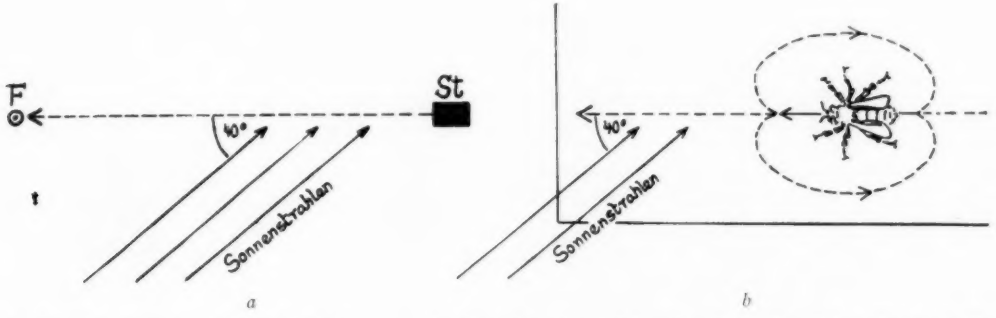

FIG. 3. The expression of direction by bees on a horizontal surface. (*a*) When flying from hive (St) to feeding place (F) the bee pays attention to the angle between the sun and its goal. (*b*) After returning to the hive the bee maintains the same angle to the sun in its wagging run on the horizontal surface and thus points the way to the goal.

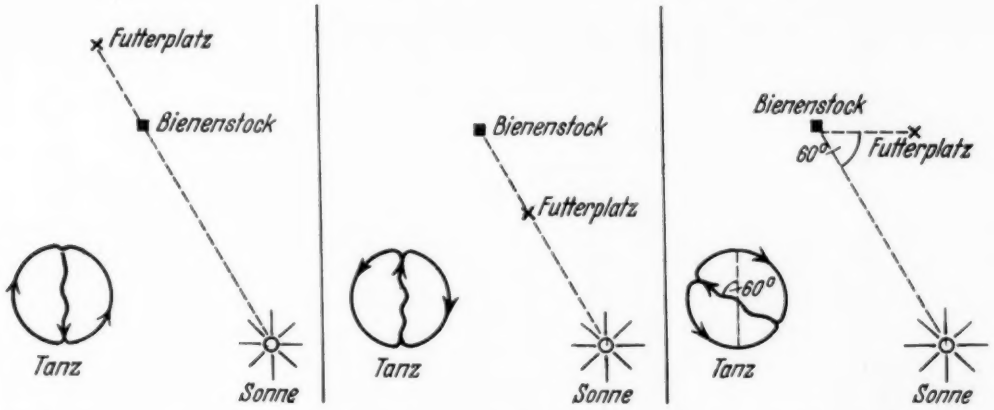

FIG. 4. The expression of direction in the dance on vertical surfaces in the bee hive. Middle: the feeding place lies in the direction of the sun, the bee moves upward in its wagging run. Right: the feeding place 60° left from the position of the sun, wagging run 60° to the left of straight upward. Left: feeding place opposite the direction of the sun, wagging run straight downward.

if a board is interposed in the sun's direction and only cloudy sky is visible in other directions.

This perception of the sun through the clouds does not depend, as one might think, upon perception of infrared light, but rather on the sensitivity of the bees to ultraviolet light. Ultraviolet between 4,000 and 3,000 Å represents a distinct color for the bee's eye, and quantitatively their greatest visual sensitivity lies in this region. If under cloudy conditions, and with the hive horizontal, one places glass filters of selective spectral transmission above the dancers, one sees oriented dances only under those filters which transmit ultraviolet light in a particular range, and disoriented dances under filters which strongly filter out the ultraviolet. Whether, and to what degree, the visible and infrared light is transmitted has no bearing on the degree of orientation of the dances (fig. 5*a* and *b*).

Should the sun stand behind a hill or be already set, the information system of the bees is undisturbed. But this is only the case if the sky is clear or at least a patch of blue sky is visible, for the blue light of the sky is to a large extent polarized, and its plane of polarization has a regular relationship to the position of the sun. Thus the bees have one more advantage over us in that they perceive the plane of polarization extremely well and can put it to use for their orientation. If the horizontal hive is shaded with a piece of fiberboard so that the bees cannot see any sky, their dances are disoriented and cannot indicate the direction of the feeding place. But if one makes a hole in the shade so that a tiny piece of blue sky is visible, for example to the north, remote from the sun, immediately their dances are precisely oriented and point to the goal. If a polaroid film is held over the dancers, one can change the direction of the dances at will by turning the polaroid. The details of these experiments prove unequivocally that it is indeed by means of the plane of polarization of the polarized sky light that the bees orient themselves. The analyser for polarized light, to which they owe this ability, is located in the sensory cells of the compound eyes.

A problem seems to arise if the bees use the sun and the related polarized light pattern of the sky as a compass to inform their comrades of the direction of a goal. The magnetic compass always points to the north, but the sun is constantly changing its position. At first I thought that it would be useful only within short intervals of time, during which the sun's position would not shift significantly. An experiment has convinced me that I was wrong. Bees can also use the sky compass over long periods; they are capable of this because they possess a remarkable sense of time and because they are familiar with the daily path of the sun. One might say that they know just where it belongs at every hour of the day.

The experiment which led to this conclusion was the following: we transported a hive of bees to an unfamiliar region, opened the flight-hole in

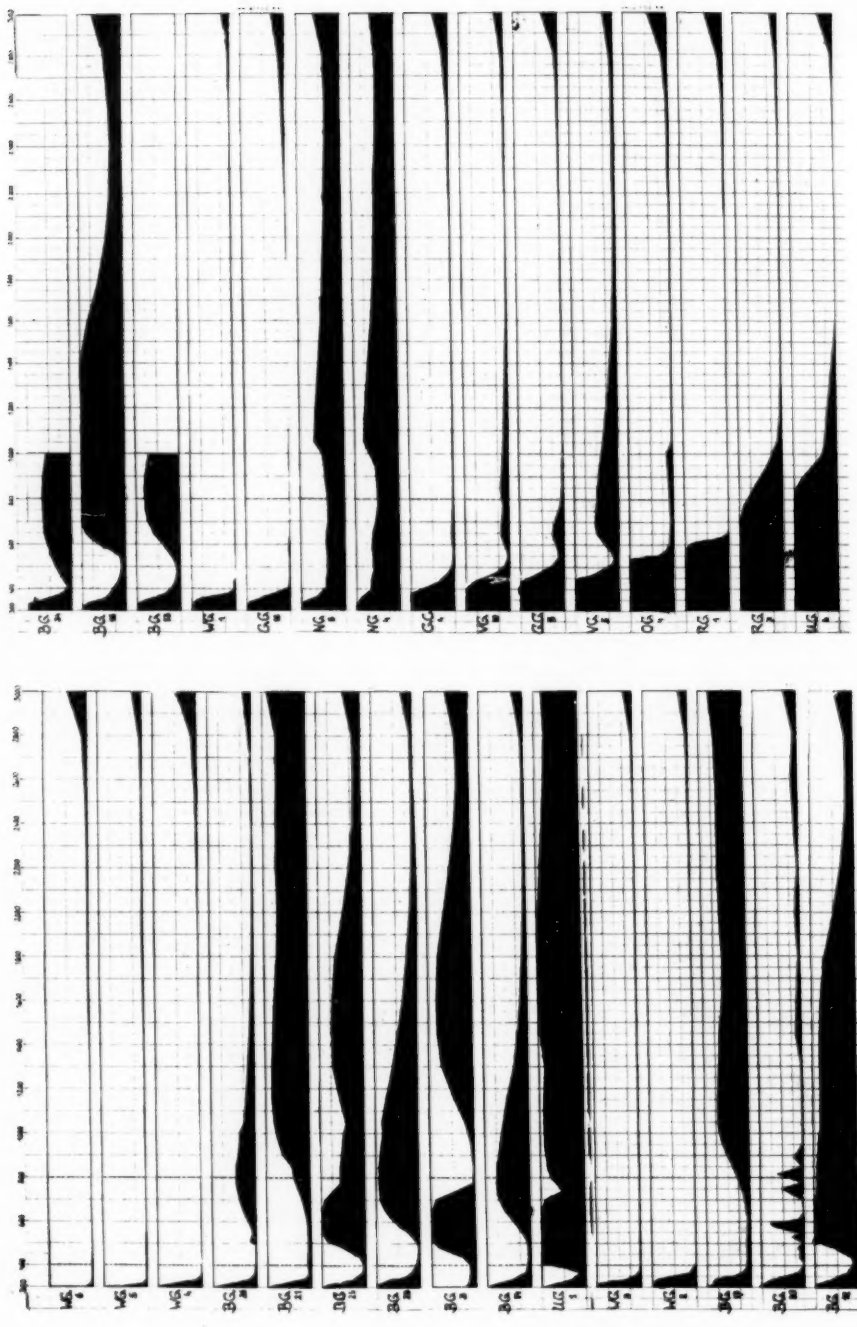

Fig. 5. Transmission of various glass filters (manufactured by Schott) in the spectral region from 300–3000 millimicrons. Under the filters of the left hand column (*a*) the bees could orient themselves by the sun even under overcast skies (though they did so only uncertainly with the five lower filters); with the filters in the right hand column (*b*) they were wholly disoriented.

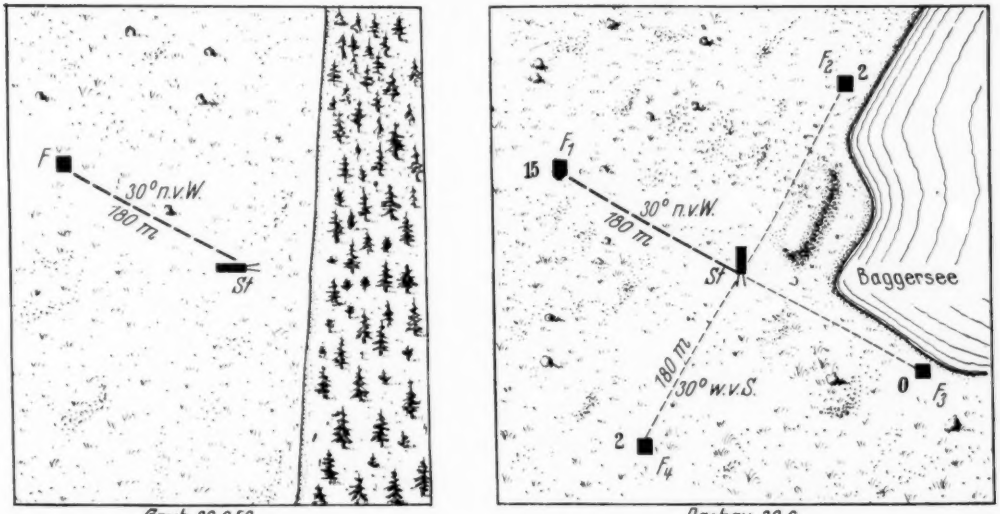

FIG. 6. (*a*) Training of numbered bees during the afternoon to fly from the bee hive (St) to a feeding place (F) 180 meters to the northwest. (*b*) The following morning the bee hive was moved to a wholly different location in territory where the bees had never been. Four feeding places (F_1–F_4) were set out. The bees searched predominantly in the accustomed direction. The figures by the feeding places indicate how many of the numbered bees came to each.

the afternoon and induced a group of marked bees to feed at a point 180 meters northwest of the hive during the afternoon and evening hours (fig. 6*a*). The next morning the hive was again moved a great distance. The new surroundings were also unfamiliar and of a completely different character. The entrance to the hive was pointed in a new direction and then was opened as on the day before. Feeding tables were placed in four directions at the same distance, 180 meters. At each feeding place sat an observer who caught every bee as soon as it arrived so that she could not send others. In a short time the collecting bees from the day before appeared in overwhelming numbers at the northwest feeding dish; they therefore had searched in the training direction (fig. 6*b*). Since they found no familiar landmarks in the unknown region, they could only have been guided by celestial navigation. And this occurred in the morning when the sun was in a completely different position from the direction in which the bees had seen it the previous afternoon and evening.

Numerous repetitions of these experiments and other types of observation besides prove that the bees can find one particular compass direction repeatedly whatever the time of day. Hence, the sun and the related polarized light pattern of the sky play an indispensable role for the bees, not only in the communication of direction, but in their general orientation as well.

A compass based on the sun's position and the polarized light pattern of the sky coupled with a reckoning of the time of day has been found in other Arthropods. The phenomenon is probably of even more general occurrence than we yet realize. But the bees remain unique in the use of the sun-compass not only for individual orientation, but also for the communication of exact information, thus placing it in the service of the community.

I certainly did not expect that the bees would help me to the great pleasure and honor which come to me today with the conferring of the Magellanic Premium by the American Philosophical Society. After all, it is these wonderful creatures who should have earned the prize rather than I, who have only described what they do.

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